Climate Change, Modelling and Conservation of the World's Terrestrial birds

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Declaration

The material contained within this thesis has not previously been submitted for a degree at Durham University or any other university. The research reported within this thesis has been conducted by the author unless indicated otherwise.

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Abstract

Global climate change is an important threat to biodiversity and is predicted to be a major driver of wildlife population extinctions throughout the current century. Across a wide range of taxa, a well-documented response to climate change has been changes in species distributions, often towards higher latitudes and altitudes. Species distribution models (SDMs) have been widely used to predict further range changes in future but their use has often focused on discrete geographical areas. Moreover, SDMs have typically been correlative, ignoring biological traits. Here, I use SDMs to project future ranges for the world's terrestrial birds under climate change. To improve the realism of projected range changes, I incorporate biological traits, including species' age at first breeding and natal dispersal range. I use these projections to predict large-scale patterns in the responses of terrestrial birds to climate change, and to explore the implications of these models for avian conservation.

There is little consensus on the most useful predictors for SDMs, so I begin by exploring how this varies geographically. With this knowledge, I develop SDMs for the world's terrestrial birds and project future species ranges using three different global climate models (CCSM4, GFDL-CM3, HadGEM2-ES) under a low (rcp26), a medium (rcp45) and a high (rcp85) representative concentration pathway. The projected ranges are used to identify species most at risk from climate change and to highlight global hotspots where species are projected to experience the highest range losses. I explore how the projected range changes affect global species communities and I identify areas where species communities are projected to change or novel communities will emerge. I assess how projected changes will affect the ability of the global Important Bird and Biodiversity Areas (IBAs) network to confer protection on the world's terrestrial bird species. Additionally, I highlight - based on projected range loss and suitable habitat and climate space beyond the dispersal range - species that will be unable to track climate change and that could be candidates for Assisted Colonization (AC). Finally, I explore the divergence between global species richness (SR) patterns and phylogenetic diversity (PD) for the world's terrestrial birds, to assess if measuring biodiversity and setting conservation targets based on SR can be expected to cover their PD as well.

Identifying the global consequences of projected range changes can inform future conservation efforts and research priorities. Changes in range extent and overlap were projected for the vast majority of the world's terrestrial birds, with one-fifth projected to experience major range losses (>75% decline in range extent projected). This has far reaching consequences for the IBA network, with an overall trend of species moving out of the IBA coverage. Furthermore 13% of the world's terrestrial birds are projected to have severe range losses that, combined with an inability to follow suitable habitat and climate space, mean they could benefit from AC as a conservation tool. Overall,

PD was found to be highly correlated to SR on a global scale; however, there are localized differences where PD is higher or lower than could be expected from SR alone. These differences suggest that considering PD could enhance conservation planning. The results demonstrate the major threat that climate change poses for the world's terrestrial bird species across all areas of the globe, and highlight the importance of considering climate change impacts to enhance their protection.

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Chapter 1

General Introduction

1. Introduction

This thesis identifies the conservation implications of the impact of global climate change on the world's terrestrial bird distributions. Both range shifts, as well as decreases in range extent, have been observed in recent decades and have been attributed to climate change (Parmesan & Yohe, 2003; Thomas *et al.*, 2004; Chen *et al.*, 2011). These range changes can have far reaching consequences for biodiversity, ranging from complete loss of suitable habitat and subsequent extinction of individual species, to the disruption of species communities, and possible cascading effects resulting in impacts on ecosystem functioning (Stralberg *et al.*, 2009; Pecl *et al.*, 2017). Additionally, the redistribution of species can affect the efficacy of protected area (PA) networks and can complicate conservation planning (Hole *et al.*, 2009; Bagchi *et al.*, 2013). Highlighting the species most at risk, and identifying the hotspots where species' ranges are most likely to be affected by climate change, can aid conservation and focuses future research efforts. This thesis is laid out in five individual manuscripts, each providing an introduction to the focal topic; consequently, this general introduction will cover only the broad background to set the research in a global context. Throughout this introduction, I will briefly introduce the projected changes in global climate. I will describe the observed and predicted impacts and risks that climate change poses for biodiversity (both in general, and for terrestrial bird species specifically). I will give a brief overview of the use of species distribution models (SDMs) to assess the impact of climate change on species' ranges. I will summarize potential impacts on the global PA networks and current efforts to evaluate and preserve their performance. I will also briefly introduce the concept of assisted colonization (AC) as conservation tool for species that are unable to keep up with climate change. Finally, I will provide an overview of additional measures of biodiversity, aside from species richness, that can be used to plan and assess conservation efforts.

1.1 Climate change

Global climate change is predicted to have far reaching impacts on biodiversity, ecosystem services, and, subsequently, human health (McMichael *et al.*, 2006; McMichael & Lindgren, 2011; Bellard *et al.*, 2012; Nelson *et al.*, 2013). Sea level rise, ocean acidification and increases in extreme weather conditions are all consequences of global warming (Easterling *et al.*, 2000b; Easterling *et al.*, 2000a; Hoegh-Guldberg *et al.*, 2007; Dangendorf *et al.*, 2017). Temperature rise has been attributed to the increase of atmospheric carbon dioxide (CO_2), which is largely driven by anthropogenic greenhouse gas emissions, for which, current levels exceed observed fluctuations throughout the past 420,000 years (Petit *et al.*, 1999; IPCC, 2001). Since 1880, the global average temperature has risen by 0.85 °C; it is likely to increase between 0.4 to 4.6 °C by 2081–2100 relative to 1986–2005 (IPCC, 2014). The predicted increase in temperature varies greatly among the different projected emission

pathways (0.3°C to 1.7°C (RCP2.6), 1.1°C to 2.6°C (RCP4.5), 1.4°C to 3.1°C (RCP6.0), 2.6°C to 4.8°C (RCP8.5)), with a projected 2°C temperature rise under the most stringent mitigation scenario (IPCC, 2014). Without urgent action to lower greenhouse gas emissions, these temperature rises are likely to lead to severe, widespread and possibly irreversible impacts by the end of the 21st century (Stocker *et al.*, 2013). The Paris agreement of 2016, a part of the United Nations Framework Convention on Climate Change, aims to address these global temperature changes by bringing together all nations in a joint effort to mitigate climate change. This agreement aims to keep the global temperature rise well below 2°C, compared to pre-industrial levels, targeting a rise of 1.5°C (Hulme, 2016). It has currently been ratified by 146 out of 195 parties (UNFCCC, 2015). Minimum climate change scenarios produced fewer predicted extinctions than mid-range or maximum scenarios; thus, minimizing greenhouse gas emissions can reduce risk for terrestrial species (Thomas *et al.*, 2004). Ecosystems are already responding to global warming (Hoegh-Guldberg & Bruno, 2010), with community disruptions and disease outbreaks attributed to climate induced range changes (Ling, 2008).

1.2 Impacts on biodiversity

Climate change is likely to affect biodiversity at all scales, including genes, species, communities and ecosystems (Leemans & Eickhout, 2004; Parmesan, 2006; Thomas *et al.*, 2006; Gilman *et al.*, 2010; Hoegh-Guldberg & Bruno, 2010). Enhancing species' risk of extinction (Thomas *et al.*, 2004; Leadley *et al.*, 2010; Pereira *et al.*, 2010; Walther, 2010; Bellard *et al.*, 2012), climate change is of particular concern for the large number of plants and animals that that occur in biodiversity hotspots, including the Caribbean, the Tropical Andes, Southwest Australia and the Cape Floristic Region (Malcolm *et al.*, 2006b).

Impacts of climate change on biodiversity are projected to be highly variable across the globe (Walther *et al.*, 2002). For example, variations in topography can lead to differential responses in vegetation cover to changes in temperature (Halm 1997). Regional changes in temperature and precipitation are highly heterogeneous, resulting in spatially heterogeneous responses of organisms, communities and populations (Walther *et al.*, 2002). In some areas, species might be able to persist in climatic refugia, although the surrounding climate becomes unsuitable (Taberlet & Cheddadi, 2002; Saxon *et al.*, 2005; Keppel *et al.*, 2012). Both novel and disappearing climates can pose threats to biodiversity, increasing extinction risk and, potentially, disrupting species communities and causing the formation of novel communities (Overpeck *et al.*, 1992; Hobbs *et al.*, 2006; Williams *et al.*, 2007). Novel climates, i.e. with no current analogues are most likely to occur in the tropics and subtropics, whilst temperate and high latitudes have a lower risk of novel climates (Williams & Jackson, 2007). The overall velocity of climate change differs across the terrestrial areas of the world

with climate shifting especially rapidly in flat landscapes, in which flooded grasslands, savannas and mangrove areas are heavily represented (Loarie *et al.*, 2009).

1.3 Species responses to climate change

Species' responses to climate change are not uniform (Walther *et al.*, 2002; Bohning-Gaese & Lemoine, 2004; Urban *et al.*, 2012). Not all species will be affected by climate change the same way, and the vulnerability of a species depends on its exposure to climate change as well as its sensitivity to climate (Dawson *et al.*, 2011; Foden *et al.*, 2013; Pacifici *et al.*, 2015). The sensitivity of a species is a combination of its adaptive capacity, based on factors like genetics and phenotypic and behavioral plasticity, as well as its resilience (e.g., the ability to recover from a disturbance might depend upon factors such as life history, population dynamics and dispersal ability) (Williams *et al.*, 2008; Dawson *et al.*, 2011; Foden *et al.*, 2013). Species might be able to persist under climate change by shifting their distributions into climatically suitable space, or through adaptation of populations to the new local climatic conditions (Berg *et al.*, 2010; Bellard *et al.*, 2012; Hoffmann *et al.*, 2015). Certain traits in species are associated with higher climate vulnerability. For example, specialist species are predicted to decline more under climate change than generalist species (Warren *et al.*, 2001; Thuiller *et al.*, 2005a). Species with a narrow range extent are overall at higher risk of extinction (Purvis *et al.*, 2000b; Payne & Finnegan, 2007) and have been found to be more vulnerable to climate change (Urban, 2015). Similarly, endemic species are projected to be more vulnerable to climate change (Dirnböck *et al.*, 2011; Urban, 2015), with rarity already exposing species to a higher extinction risk (Pimm *et al.*, 1988; Gaston, 1994). Finally, low natal dispersal ability has been associated with a high risk of being unable to track climate change (Foden *et al.*, 2013). Responses to climate change vary across species, and can include range shifts, behavioral modifications and genetic adaptation (Menzel *et al.*, 2006; Parmesan, 2006; Alberto *et al.*, 2013). In the following paragraphs, I will briefly introduce species responses in terms of range and community changes.

Species responses to climate change – range changes

Evidence for climate change impacts on species distributions can be found in fossil data (Pitelka *et al.*, 1997), with the earliest proof of climate driven range changes coming from mismatches between current distributions and the distribution of plant and animal fossils (Diffenbaugh & Field, 2013). In response to previous ice ages, species have often demonstrated substantial range shifts. For example, the peninsulas of Europe were major climate refugia during the Pleistocene Ice Age and species spread out northwards when the ice retreated 16000 BP (Hewitt, 1999). More recently, shifts across all taxa have already been shown, with species typically moving towards higher altitudes and latitudes in response to current climatic changes (Parmesan *et al.*, 1999; Parmesan & Yohe, 2003; Hickling *et al.*, 2006; Kelly & Goulden, 2008; Thomas, 2010). Species range shifts are

most pronounced in areas that are undergoing the fastest warming, such as those at high latitudes (Chen *et al.*, 2011; Tayleur *et al.*, 2016). The median velocity of these range shifts has been estimated at 11 meters per decade for altitudinal shifts and 16.9 km for latitudinal range shifts, but range shifts vary greatly between different species (Chen *et al.*, 2011). Although rapid range shifts have been observed under climate change, some species have been found to be lagging behind climate change (Menéndez *et al.*, 2006; Devictor *et al.*, 2008). These lags behind the climate have different causes: species might not be able to move through fragmented habitat; they might be inhibited by their low natal dispersal ability; they might have a very long generation time, resulting in slow demographic responses; or they might be slowed by biotic interactions (Hill *et al.*, 1999; Cahill *et al.*, 2012; Schloss *et al.*, 2012; Pearce-Higgins & Green, 2014). As well as shifts in ranges, range contractions have been shown for various species (McClean *et al.*, 2005; Wilson *et al.*, 2005; Moritz *et al.*, 2008). More generalist species and species with very high dispersal ability, however, have been projected to have potential to extend their ranges when climate becomes more favourable (Hill *et al.*, 2002; Dullinger *et al.*, 2004; Hallinger & Wilmking, 2011). Climate change can affect species range boundaries directly (having direct impact on recruitment and mortality) or indirectly through changes to species interactions or climate-driven changes to the physical structure of habitats (Thomas, 2010). Throughout this thesis I investigate the direct impacts of climate change onto species range boundaries, including changes in range extents as well as range shifts. In this context species responses to climate change refer to range changes, which are ultimately a result of demographic responses, including patterns of birth and death, and the individual dispersal ability of a species.

Species responses to climate change – biotic interactions and communities

The individualistic responses of species to climate change lead to changes in species community compositions and can cause entirely novel community compositions (Ackerly, 2003; Williams & Jackson, 2007; Urban *et al.*, 2012; Gallagher *et al.*, 2013). In particular, novel climates are likely to lead to non-analogue communities (Overpeck *et al.*, 1992; Williams & Jackson, 2007). Butterfly species have shown individualistic responses, moving to higher altitudes at highly heterogeneous rates, leading to changes in species community composition, with a greater number of high elevation specialists going extinct than new species colonizing (Wilson *et al.*, 2007). These changes in community composition affect species' biotic interactions, leading to changes in spatial pattern, and can have far reaching impacts (Walther, 2010). Possible consequences are changes in the competitive balance particularly between species that lack a co-evolutionary history (Urban *et al.*, 2012); changes to or disruptions of the food web (Schweiger *et al.*, 2008), affecting prey abundance, with prey species declining and less prey being available (Durance & Ormerod, 2010) and predator

densities (Harley, 2011); and changes in the trait composition of a community (Gallagher *et al.*, 2013). Again, responses across species in a community are not entirely idiosyncratic, with specialists being more likely to struggle than generalists (Lurgi *et al.*, 2012). Overall, changes in community compositions are likely to impact trophic interactions, and have consequences for ecosystem functioning (Tilman *et al.*, 1997; Loreau *et al.*, 2001; Hooper *et al.*, 2005; Suttle *et al.*, 2007; Walther, 2010). Due to their high unpredictability, novel species communities can pose a challenge and it is important to identify areas where they are likely to occur (Stralberg et al., 2009).

1.4 Climate versus land use change and human disturbance

Humans have been altering habitats and affecting biodiversity for a long time. As a consequence, one quarter of the world's birds have gone extinct over the last two millennia (Steadman, 1995). Today, anthropogenic land use change is the main driver of loss of biological diversity worldwide, and the leading cause of habitat loss and extinction in vertebrates (Vitousek *et al.*, 1997; Hoffmann *et al.*, 2010). In particular, the world's tropical rainforests have been severely affected by habitat loss through deforestation (Dale *et al.*, 1994; Brook *et al.*, 2003; Achard *et al.*, 2014). Thus, in the tropics land use change might outweigh climate change as the principal future threat to species (Jetz *et al.*, 2007). In addition to being a major threat to biodiversity, land use change also interacts with climate change, and can amplify its impacts by affecting landscape permeability and reducing habitat heterogeneity (Oliver & Morecroft, 2014). A study on butterflies in the UK showed that climate has become more suitable over the last 30 years, but habitat loss has caused declines in most populations (Warren *et al.*, 2001). Land use change is also the second major driver of changes in community compositions after climate change, although the relative importance of climate and land use change in causing non-random community changes varies across different habitats (Kampichler *et al.*, 2012).

1.5 Terrestrial bird species as a model taxa

Birds are one of the most widely-studied taxon, with intensive monitoring resulting in spatially diverse and robust data sets (Bonnet *et al.*, 2002; Ducatez & Lefebvre, 2014; Pearce-Higgins & Green, 2014). Their wide distribution and occurrence in nearly every habitat make them useful indicators for studies on richness patterns and environmental change (BirdLife International, 2013). Bird species show individualistic responses to climate change in space and time (Bohning-Gaese & Lemoine, 2004). A variety of responses of bird species to climate change has been documented, with projected losses in their breeding (Wauchope *et al.*, 2017) and non-breeding ranges, in both range extent (Barbet-Massin *et al.*, 2009; Doswald *et al.*, 2009) as well as observed abundance (Wilson *et al.*, 2011). As with other taxa, birds have been shown to track suitable climate space, often moving their ranges towards higher latitudes (Thomas & Lennon, 1999; Brommer, 2004; Zuckerberg *et al.*,

2009) and altitudes (Archaux, 2004; Hickling *et al.*, 2006; Tingley *et al.*, 2012). However, the range shifts of some bird species have been found to lag behind the rate of climate change. A study on breeding birds in France found that, whilst their climate envelope has moved 273 km across France throughout two decades, the bird communities had shifted only about 91km (Devictor *et al.*, 2008). Those changes in avian species distributions are projected to reshuffle avian communities in many areas across the globe, with high predicted turnover in the western hemisphere for mountainous areas such as the Andes but also in the Tundra at high northern latitudes (Lawler *et al.*, 2009; Pearce-Higgins & Green, 2014). Anticipated changes in species ranges are projected to result in loss of functional diversity across avian species communities globally (Barbet-Massin & Jetz, 2015). Furthermore, changes in the phenology of avian species in response to climate change have been demonstrated, such as the earlier arrival of migrant species on their breeding grounds (Visser & Both, 2005; Møller *et al.*, 2008; Pearce-Higgins *et al.*, 2010). As well as the threats resulting from climate change, birds are threatened by land use change (Gaston *et al.*, 2003), with as many as 400 species being projected to lose more than 50% of their habitat by 2050 (Jetz *et al.*, 2007).

1.6 Species distribution models and their application to studying the impacts of climate change

Analyses of the species–environment relationship have been a central topic in ecology since the early 19th century (Guisan & Zimmermann, 2000). Species distribution models (SDMs), or ecological niche models, model the statistical relationship between a species' geographic distribution and a suite of bioclimatic variables (Guisan & Thuiller, 2005). As a result of recent computational and methodological advancements, their use within the ecological community has grown exponentially since the 1990s (Franklin 1995). SDMs are based on the principle of the realized niche, the set of "environmental conditions (abiotic factors) under which a species is able to maintain viable populations without immigration" (Grinnell, 1917; Hutchinson & MacArthur, 1959). SDMs link the observed range of a species to the environmental variables in the area (Keith *et al.*, 2008). This allows the prediction of future distributions by applying the species-climate relationship to future climate scenarios, to identify regions which will be habitable for the species (Heikkinen *et al.*, 2006). SDMs have been used extensively to predict the impact of future climate change on species distributions (Thuiller *et al.*, 2005b; Araújo & Rahbek, 2006; Huntley *et al.*, 2006; Lawler *et al.*, 2009). Today, SDMs are increasingly used in studies for conservation planning and climate adaptation strategies (Araújo *et al.*, 2006; Hole *et al.*, 2011; Swanson *et al.*, 2012). In this context, SDMs can be valuable tools with which to identify species' threats from climate change (Barbet-Massin *et al.*, 2012a) and to evaluate the impact that climate change will have on the coverage of species by

protected area networks (Araújo *et al.*, 2004; Hole *et al.*, 2009; Araújo *et al.*, 2011; Bagchi *et al.*, 2013; Virkkala *et al.*, 2013; Baker *et al.*, 2015).

Limitations of species distribution models

Although SDMs are widely used in ecology and are highly useful for evaluating the impacts of climate change on species ranges and supporting conservation planning, they do have limitations. These limitations are widely recognized (Araújo & Guisan, 2006; Araújo & Peterson, 2012) and need to be considered when applying SDMs and interpreting projected distributions. Awareness needs to be paid to the basic assumption of an SDM: that the data on which the model is built describe the full climatic niche of a species; if species do not fill their entire niche, due to biotic interactions, the predictive power of an SDM is limited (Araújo & Guisan, 2006). Novel climates add to this challenge, since the climatic niche of a species might not be fully described by the current data used to build the model (Williams & Jackson, 2007; Fitzpatrick & Hargrove, 2009). This can also be a challenge for species with a very narrow range extent. Species endemic to small oceanic islands, or those that occur in a single lake are obvious examples of where range extent is not directly related to climate (Thomas, 2010). For species with ranges largely shaped by interspecific interactions, bioclimatic models will be less accurate for projecting potential range shifts under climatic change (Lawler *et al.*, 2009). Competition can slow the advance of colonizing species and, thus, can cause lags in climate tracking, which might not show in range predictions based on the climatic niche (Urban *et al.*, 2012).

Additionally, both current and future climate data can introduce uncertainty resulting from the variability between datasets (Beaumont *et al.*, 2008; Baker *et al.*, 2016) as well as the approach used to process and downscale the data (Baker *et al.*, 2017). The predictions from different SDM types can be highly variable (Elith & Graham, 2009). One way to improve the predictions is to use ensemble modelling to produce a consensus of the predicted distributions derived from the different modelling types (Araújo *et al.*, 2005a; Marmion *et al.*, 2009). Two more technical challenges are the spatial extent from which the absence data are drawn and potential spatial autocorrelation of ecological data, the latter of which violates the assumption of independence, undermining the statistical analysis if it is not addressed (Lichstein *et al.*, 2002; Dormann, 2007). Finally, the choice of bioclimatic variables to model a species distribution can introduce uncertainty into the predictions and can be especially challenging when modelling large numbers of species (Barbet-Massin & Jetz, 2014). This has found surprisingly little attention in the SDM literature so far (Synes & Osborne, 2011; Braunisch et al., 2013). Keeping these limitations in mind, SDMs are a very useful tool to identifying exposure to climate change (Dawson *et al.*, 2011).

1.7 Protected areas and species conservation under climate change

Between 10 and 15% of the earth's surface is under some kind of protection, safeguarding some of the world's most imperiled biodiversity (Chape *et al.*, 2005; Soutullo, 2010). Still, the protected area (PA) network is far from complete (Rodrigues *et al.*, 2004b; Venter *et al.*, 2014). Without conservation intervention, species can rapidly go extinct (Sinervo *et al.*, 2010). Furthermore, climate change is posing new threats to biodiversity by causing loss of species' protected area coverage (Téllez-Valdés & D¡Vila-Aranda, 2003). Due to the static nature of the protected area network, species are likely to move in and out of PA boundaries under climate change (Hannah, 2008). For some PAs, rates of local colonisation may counteract losses, maintaining the importance of those areas; however, this is not always the case (Gillingham *et al.*, 2015). Reductions in biodiversity coverage have been projected for a wide array of PAs across country as well as continent wide networks (Araújo *et al.*, 2004; Coetzee *et al.*, 2009; Hole *et al.*, 2009; Araújo *et al.*, 2011; Bagchi *et al.*, 2013; Virkkala *et al.*, 2013; Baker *et al.*, 2015). Not only has species richness been projected to reduce within protected areas but, also, species' abundance (Johnston *et al.*, 2013). Additionally the occurrence of disappearing and novel climates will cause challenges for conservation management in these areas (Wiens 2011).

Adapting protected area networks to climate change

A variety of potential management strategies has been suggested to adapt protected area networks to climate change. Firstly, it is important to model the impacts of climate change onto the protected area network and to assess the change (Hannah *et al.*, 2002). Useful modelling tools to assess the overall impact of climate change on biodiversity, across a protected area network, are general circulation models (GCMs), regional climate models or dynamic vegetation models (Hannah et al, 2002). Furthermore SDMs can support conservation planning by providing species specific information about changes in protected area coverage (Hannah et al, 2002). Following this, suggested steps to ensure future coverage of biodiversity include: creating additional reserves to compensate for the losses in coverage under climate change, which can be based on minimum coverage of species or representation of climate (Pressey & Cowling, 2001; Hannah, 2008); reclassifying the existing areas and replacing ineffective areas instead of adding new ones, which can be more cost efficient (Fuller *et al.*, 2010; Alagador *et al.*, 2014); temporal alteration of PAs' protection status or mobile protected areas, to facilitate range changes (Soto, 2002; Hannah, 2008); or increasing connectivity between PAs and introducing stepping stones, which is another cost efficient solution (Williams *et al.*, 2005; Saura *et al.*, 2014). All of the afore mentioned conservation strategies rely on a good spatial understanding of the climate change impact on the species communities within the PAs in a network and their stability under climate change.

Assisted colonization

For some species, improvements to the PA network and the facilitation of movements between PAs will not be enough to prevent their extinction. Species with low natal dispersal ability, in particular, are likely to be unable to keep up with the velocity of climate change (Midgley *et al.*, 2002; Broennimann *et al.*, 2006). Other species might be prevented from dispersing through the landscape by human barriers (Mc Lachlan 2007). For these species, assisted colonization (AC), the translocation of species into suitable habitat and climate space beyond their natal range, has been widely discussed in recent years (Hunter, 2007; Hoegh-Guldenberg *et al.*, 2008; Ricciardi & Simberloff, 2009b; Thomas, 2011). Although there are strong arguments for the artificial movement of these species to avoid their extinction, there are also risks (Mueller & Hellmann, 2008; Ricciardi & Simberloff, 2009a), to both the target species and the recipient community (Chauvenet *et al.*, 2013b), and ethical arguments (Minteer & Collins, 2010; Sandler, 2010; Schwartz *et al.*, 2012) that make AC a very controversial conservation tool. So far it is not known how many threatened species could actually benefit from this conservation tool (Thomas, 2011).

1.8 Measuring biodiversity

Species richness is the most frequently used measure of biodiversity (Gaston, 1996; Gotelli & Colwell, 2001), and is often the basis on which conservation plans are made and PAs are planned. In recent years it has been widely discussed whether species richness (SR) alone is a sufficient indicator to select areas for the conservation of biodiversity (Faith, 2002; Orme *et al.*, 2005; Forest *et al.*, 2007; Helmus *et al.*, 2007; Isaac *et al.*, 2007). Maximising phylogenetic diversity (PD) has been suggested as a key for conservation decisions (Isaac *et al.*, 2007), as it is a useful indicator for the evolutionary potential of a community (Faith, 1994). The most frequently used measure of PD in a conservation context, is Faith's PD, which summarizes how much of the branching pattern of the phylogenetic tree is represented within a community, by adding the branch length of all members of the community (Faith, 1992). Recent advances in the construction of phylogenetic super trees facilitate comparisons between SR and PD for large groups of species or even entire taxa (Barker, 2002). Although SR has been found to be a good surrogate for PD, in general, evidence from mammals and amphibians (Davies & Buckley, 2011; Fritz & Rahbek, 2012) suggests that the two measures are not entirely congruent, with localized differences where PD is unexpectedly high or low. It is not known if SR and PD are congruent for the world's birds and, thus, if SR can be expected to automatically cover PD when used as a measure for conservation planning.

1.9 Project aims

Several gaps in current knowledge emerge from the above review and form the basis for this thesis. Here, I reiterate those gaps and describe the structure of the following chapters.

1. To identify hotspots for climate change impacts on avian diversity

Firstly, I identify climatic variables that perform well for modeling bird distributions on a global scale. Using the selected climatic variables, I model the distribution of all terrestrial bird species under climate change. I identify hotspots where climate change is projected to have the highest impact on the ranges of terrestrial bird species and I highlight species groups whose ranges are projected to be most affected by climate change. Using the projected impacts on species ranges, I identify areas where species communities are likely to be disrupted, resulting in major changes in community composition, or the emergence of novel communities.

2. To determine how projected changes in bird distributions affect the protected area network

Changes in species range extents under climate change can lead to changes in the coverage PAs provide for biodiversity. I use the projected terrestrial bird ranges to identify changes in the coverage provided by the Important Bird Area (IBA) network. I estimate the future performance of the network by comparing the coverage of current and future terrestrial bird diversity. Additionally, I flag up areas that are projected to have a high turnover in their communities and areas that are projected to have very stable community compositions under climate change. I subsequently identify which areas are projected to increase, decrease or remain of similar value for species conservation, based on their proportion of emigrating and colonizing species.

3. To identify candidate species for assisted colonization

A species' ability to persist under climate change depends on its ability to track suitable climate space. Here, I identify species that, based on their natal dispersal ability, are unlikely to keep up with the velocity of climate change. I identify species that are projected to experience serious range losses, but have substantial suitable habitat and climate space beyond their natal dispersal range. These species could be candidates for future assisted colonization. I assess how many candidate species there are, where they are located, and what attributes they have in common. The latter attributes are potentially associated with a low ability to track suitable climate space.

4. To compare species richness and phylogenetic diversity as biodiversity measures for conservation

Species richness (SR) is commonly used to identify hotspots for biodiversity, and is the measure I have used throughout this thesis. It is generally observed to correlate strongly with phylogenetic diversity (PD) of communities, but localized differences have been observed for some taxa. Here, I investigate how avian SR and PD correlate on a global scale, and I identify drivers of the observed differences.

Chapter 2

Selecting bioclimatic predictors to model global bird distributions

2.1 Abstract

Species distribution models (SDM) are frequently used to project potential range alterations under climate change. SDM methods have been widely reviewed in the research literature, where potential sources of uncertainty have been identified and methods to measure and reduce that uncertainty have been suggested. One aspect of such models that has been discussed relatively little, is the choice of bioclimatic variables used to model species distributions. Ideally, the choice of bioclimatic variables should be based on expert knowledge about the species but often these data are not available. When modelling large assemblages of species, the choice of relevant bioclimatic variables can be challenging. Here I use a subset of 400 birds from across the world to test if variable combinations exist that performs well for the majority of the world's birds. I explore the utility of a range of bioclimatic variables that are provided by the major source of such data (WorldClim) for SDMs. I run general additive models (GAM) on sensible variable combinations and identify sets that perform well for the majority of the species.

I found that a combination of variables comprising temperature seasonality, maximum temperature of the warmest period, annual precipitation and precipitation seasonality performed best overall, although several related variable combinations also had high model performance. The importance of the individual variables varied for species of different latitudinal bands, with temperature variables being more important at high latitudes. The results suggest that for studies on a global extent, where ecological expertise on the modelled species is not available, the chosen bioclimatic variable combination is a good substitute.

2.2 Introduction

Species Distribution models (SDMs) are the most widely used tool to assess the impact of climate change on species' ranges and to forecast shifts in their distribution (Thuiller, 2004; Huntley *et al.*, 2006; Barbet-Massin *et al.*, 2012a; VanDerWal *et al.*, 2013). They are increasingly used to predict range changes not only for individual species but across assemblages of species, of various taxa, to identify general patterns in distribution changes (Araújo *et al.*, 2004; Lawler *et al.*, 2009).

SDMs are based on the ecological niche concept (Hutchinson 1957) and relate species occurrences to environmental variables, using a variety of different modelling approaches (Guisan & Zimmermann, 2000). If the SDM is used to infer potential future distributions based on the climatic niche of a species, typically a statistical model is used to relate the recent distribution of a species to contemporary climatic conditions. The resultant model can then be applied to future climatic scenarios, under the assumption of niche conservatism (Pearson & Dawson, 2003; Thuiller, 2003; Wiens *et al.*, 2010). In recent years various sources of uncertainty in such models have been described, which impact the accuracy and robustness of their predictions. Among the sources contributing to model uncertainty are:

1. differences in the predictions resulting from applying different model algorithms or different implementations of the same technique (Thuiller, 2004; Pearson *et al.*, 2006; Elith & Graham, 2009);
2. the lack of absence data and potential bias in the selection of pseudo-absences (Barbet-Massin *et al.*, 2012b);
3. the spatial autocorrelation of the environmental variables (Lichstein *et al.*, 2002; Dormann *et al.*, 2007);
4. the choice of, and variability between, different baseline climate datasets (Baker *et al.*, 2016) or General Circulation Models (Beaumont *et al.*, 2008), and:
5. the climate down-scaling approach used (Baker *et al.*, 2017).

One aspect of uncertainty that, until recently, has been given relatively little consideration in SDMs is the uncertainty introduced by using different climatic predictor variables in models. However, the importance of the predictor variable choice in producing meaningful predictions, and the lack of a framework to make informed decisions when selecting climatic variables, have been recognized (Franklin, 2009; Austin & Van Niel, 2011). Furthermore recent studies have highlighted that different combinations of bioclimatic predictors included in SDMs can result in very different predictions (Synes & Osborne, 2011; Braunisch *et al.*, 2013; Barbet-Massin & Jetz, 2014). A plausible causal relationship must exist between any predictor variables used and the species' occurrence (Austin, 2002). Ideally, the choice of variables used in an SDM should be based on expert knowledge about

the relevance of the available variables to the modeled species. However, such knowledge is rarely available (Mac Nally, 2000). An alternative approach to choosing suitable predictor variables in SDMs is to use model selection, although this approach cannot fully substitute the preliminary variable selection based on ecological knowledge (Mac Nally, 2000). Studies have found that different combinations of bioclimatic variables, which have a similarly high model-fit when tested on contemporary data, can produce very different projections, especially when projecting into novel climatic space (Synes & Osborne, 2011; Braunisch *et al.*, 2013). Additionally variables can also differ in their importance (even within a single species) across space and scale (Menke *et al.*, 2009).

Despite the concerns raised above, the vast majority of studies using SDMs fail to justify their selection of predictor variable. Porfirio et al (2014) found through extensive review of the current SDM literature, that the most commonly used approaches are: (1) to use all variables available in the model, (2) to use all variables available but to consider collinearity, and exclude highly correlated variables, or, more rarely, (3) to select variables based on ecological knowledge.

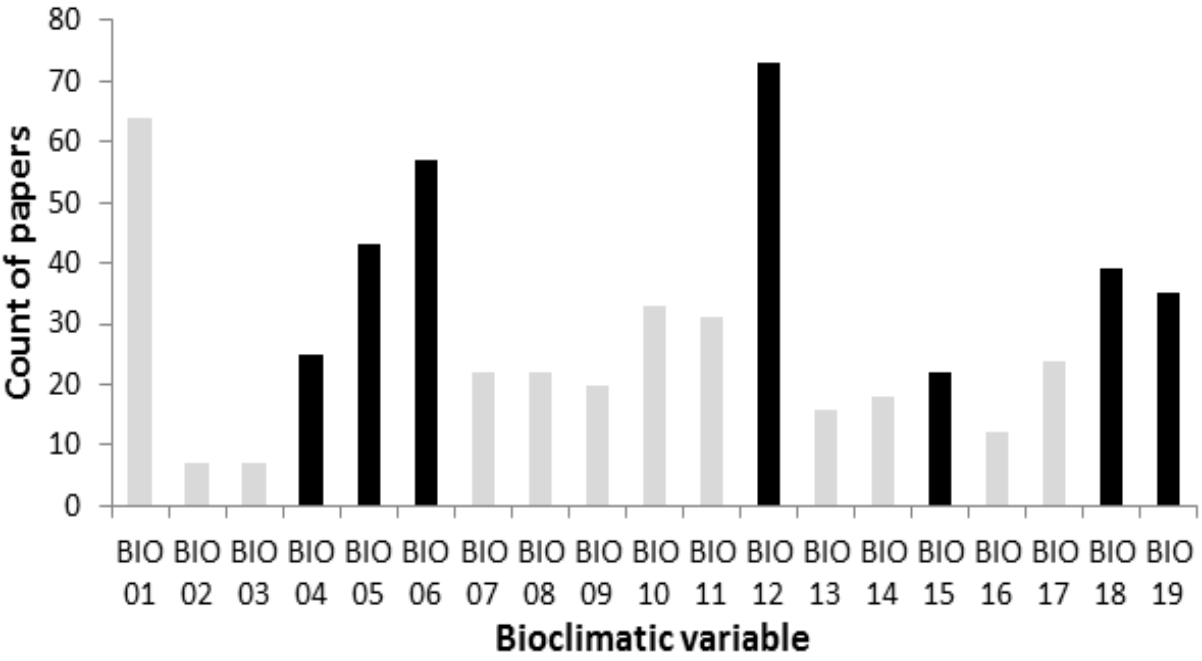


Figure 2.1: The frequency of the bioclimatic variables used in papers modelling species distributions. 183 papers were reviewed for the study listing the predictor variables used in SDMs. Figure adapted from Porfirio (2014) to only include bioclimatic variables. Black bars represent the variables that were selected to be tested in the models.

Bioclimatic variables that are very frequently linked to determine species ranges are annual mean temperature and annual mean precipitation, as well as measures of the maximum and minimum temperature of the warmest/coldest period and precipitation of the warmest/coldest quarter (Figure2.1, Full description of bioclimatic variables see Table 2.1; data available from Porfirio *et al*. 2014).

For studies involving large numbers of species, selecting species-specific bioclimatic variables for models is especially challenging. For many/most species, the ecological knowledge required to select appropriate bioclimatic variables to define their niche limits does not exist. Additionally, using a model selection approach for individual species is computationally intense, and hence often impractical, across large species groups. Such approaches can occasionally result in the chance selection of inappropriate variables that just happen to help explain a species range limits (Lennon, 2000; Dormann, 2007). However, the risk of chance correlations is much less problematic when the model building and test data are not spatially auto-correlated. Another commonly applied approach to select bioclimatic variables is to select variables associated with known physiological limits to groups of species (Thuiller *et al.*, 2005b; Araújo *et al.*, 2006). Whilst this latter approach is appealing, it does still presuppose knowledge of limiting factors in ecosystems, which could be based on only sparse evidence. Here, I use a combination of the two approaches, pre selecting bioclimatic variables that have been frequently linked with limiting species ranges and then using a model selection approach for the final selection of the best performing combination of bioclimatic variables.

I use a subset of 400 bird species whose ranges are distributed relatively evenly across the globe, and which represent species from all latitudinal bands and species of varying range extents. This even distribution of range centers across the globe is important, since the climatic properties that limit species ranges differ across different latitudes. According to the species energy hypothesis, the limiting factor at high northern and southern latitudes is energy (temperature) whereas at medium latitudes it is moisture availability (Wright, 1983). To assess if a variable combination works for a global study, incorporating birds with ranges at all latitudes, it is important to get species from all latitudes into the sample. I compile combinations of three and four bioclimatic variables, based on those that are frequently used to predict species' ranges and after considering collinearity. I then fit SDMs for each of the 400 selected species using all of the variable combinations and compare their performance across species using a model selection approach. The aim is to identify whether a single combination of bioclimatic variables can be used to model the distribution of the majority of the world's terrestrial birds, or whether particular subsets of bioclimatic variables routinely perform better at predicting species ranges in different areas of the world.

2.3 Methods

2.3.1 Species distribution data

I obtained global breeding range polygons from BirdLife International for 400 bird species (BirdLife International & NatureServe, 2012). The subset of species was drawn using stratified random sampling based on the centre point of the distribution of a species, so that I had an even representation of species globally (Figure 2.1). The distribution data were intersected with a 0.5° degree (55 x 55 km at the equator) resolution grid. Species were considered present in a cell if their polygon overlapped at least 10% with the underlying grid cell.

Sampling absences too narrowly around the edge of a species' range limits the sampled climate space and, thus, can truncate the environmental response curve (Thuiller *et al.*, 2004; Barbet-Massin *et al.*, 2012b). I selected pseudo-absence data for each species using a distance-weighted approach. Absences were selected randomly from beyond a species range margin but following a declining probability of $\frac{1}{D_e{}^2}$ whereas D_e is the distance from the edge of a species range. This approach aims to balance the selection of pseudo-absence data from too narrowly around a species range, whilst also minimising selecting absence points from areas very distance from the range edge, where absence could be due to non-climatic factors e.g. dispersal limitations. Our approach also minimises the selection of pseudo absences from geographically distant points that might contain little useful information for the model (Anderson & Raza, 2010). I used an equal number of presences and absences to build models for each species. However, for species with a range of fewer than 1000 cells I selected 1000 pseudo-absence points for the species. This minimum number of pseudo-absences was chosen to reduce the risk of restricting model performance of the general additive models (GAM) due to a low number of pseudo absences (Barbet-Massin *et al*., 2012b). For each species I derived five sets of pseudo-absences for modelling purposes.

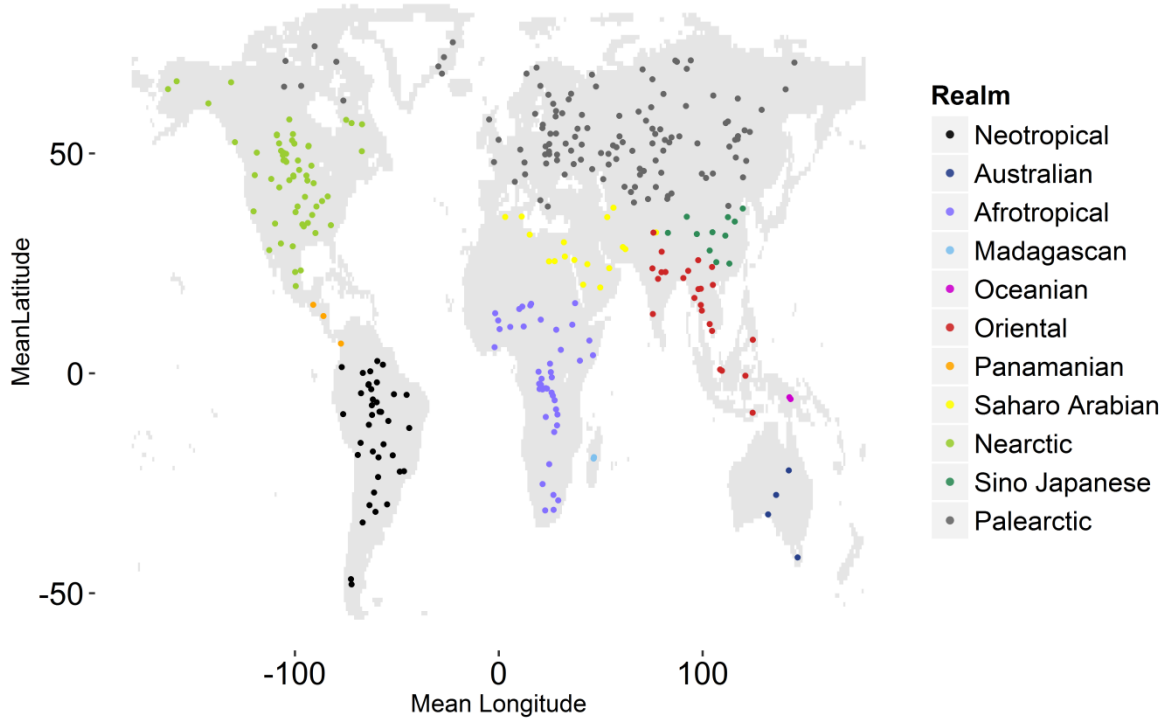


Figure 2.1: Range centroids for the 400 focal species. Colours are indicating the different zoogeographic realms of Holt *et al.* (2013) in which each range centroid is located in.

2.3.2 Contemporary climate data

I obtained 19 bioclimatic variables from Worldclim (Hijmans *et al.*, 2005, http://worldclim.org/) as potential explanatory variables (Table 2.1). I up-scaled the bioclimatic data to a 0.5° degree grid to match with the gridded species distribution data. I then pre-selected 12 of these as potential explanatory variables of species ranges, based on those most frequently used in the SDM modelling literature across a broad variety of species (See Figure 2.1 and Supplementary material Table S2.1), excluding variables that were highly correlated (>0.7) with other variables (for example, annual mean temperature is highly correlated with all other temperature variables, Figure 2.2). After this process seven potential variables remained. These were: temperature seasonality, maximum temperature of the warmest period, minimum temperature of the coldest period, annual precipitation, precipitation seasonality, precipitation of the warmest quarter and precipitation of the coldest quarter. I produced SDMs based on all possible combinations of three and four variables, again avoiding combinations of variables that had a Pearson's correlation coefficient of >0.7 with other variables in the models (Dormann *et al.*, 2013). This resulted in 23 possible variable combinations (7 four-variable combinations and 16 three-variable combinations; see Supplementary material, Table S2.2).

Table 2.1: Bioclimatic variables extracted from Worldclim (Hijmans *et al.*, 2005, http://worldclim.org/). The variables highlighted were selected to be tested in the models.

WorldClim code	Variable name	How is the variable derived
BIO1	Annual mean temperature	-
BIO2	Mean diurnal range	Mean of monthly (max temp – min temp)
BIO3	Isothermality	(BIO2/BIO7) * 100
BIO4	Temperature seasonality	Standard deviation * 100
BIO5	Maximum temperature of the warmest period	-
BIO6	Minimum temperature of the coldest period	-
BIO7	Temperature annual range	BIO5-BIO6
BIO8	Mean temperature of the wettest quarter	-
BIO9	Mean temperature of the driest quarter	-
BIO10	Mean temperature of the warmest quarter	-
BIO11	Mean temperature of the coldest quarter	-
BIO12	Annual precipitation	-
BIO13	Precipitation of the wettest period	-
BIO14	Precipitation of the driest period	-
BIO15	Precipitation seasonality	Coefficient of variation
BIO16	Precipitation of the wettest quarter	-
BIO17	Precipitation of the driest quarter	-
BIO18	Precipitation of the warmest quarter	-
BIO19	Precipitation of the coldest quarter	-

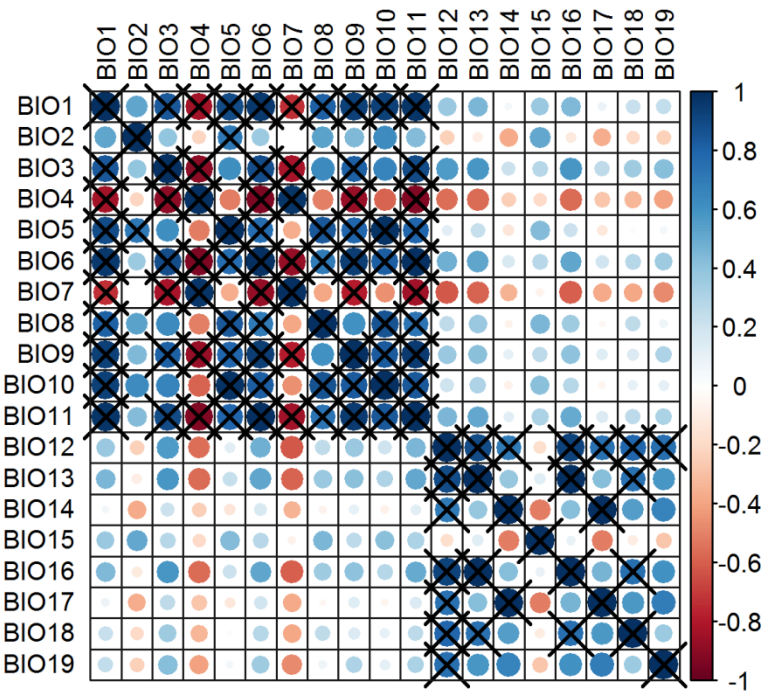


Figure 2.2: Correlation matrix of the bioclimatic variables from the WorldClim dataset. Blue indicates a positive correlation, red indicates a negative correlation, colour shade and circle size indicate the strength of the correlation. Crossed out combinations have a correlation > 0.7 and cannot be used in the same model.

2.3.3 Species distribution models

To compare the performance of these different variable combinations among the 400 species I produced SDMs for each species for each variable combination. I applied general additive models (GAMs), using thin-plate regression splines (Wood, 2003; Wood, 2006) to model the relationship between species' occurrence and the three or four bioclimatic variables. I used the 'gam' function of the 'mgcv' R package, fitting a Bernoulli response, using a logit link (Wood, 2011; R Developement Core Team, 2012).

Spatial dependence

To deal with the spatial dependence of the data I used a blocking approach following the methods of Bagchi *et al.* (2013). The data were split into sampling units based on the world's ecoregions (Olson *et al.*, 2001). I then collated these sampling units into 10 blocks of approximately equal extents, each of which fully represented climate parameter-space. Models were subsequently built using data from nine blocks and the performance was assessed based on the (spatially semi-independent) left-out tenth block. This process was repeated 10 times leaving out a different block each time. For each model, I evaluated the performance of SDMs based on the different variable subsets, using the 'area

under the curve' (AUC) (Fielding & Bell, 1997) of the model when applied to independent blocks of data as our metric of model fit. Using this approach, I ranked the variable combinations by the frequency with which they came up as one of the best models (from AUC) for a species, when applied to blocks not used in model-fitting. I then summed the number of times that different variable subsets produced the best, second-best etc. fitting models as a measure of how the variable subsets performed overall, in terms of being able to define species distributions. I also explored how the SDMs based on different variable subsets performed in relation to the latitude of species ranges. I split the species into three groups according to the latitude of their range centroid as follows: centroids above 23.5° latitude, centroids between 23.5° and -23.5° latitude (the tropics) and centroids below -23.5° latitude and explored difference in the top variable combinations in the different latitudinal bands.

Variable importance

To extract a metric of relative importance of the individual variables used to model species distributions, I contrasted AUC values of the different three- and four-variable combinations with and without a focal variable. I used the decline in AUC value between the four-variable and the three-variable model as an indicator for the importance of the variable missing from the latter. To test if there was a significant difference in the relative variable importance, based on the mean decline in AUC after dropping each variable individually, I used a one-way analysis of variance (ANOVA). Once I found a significant difference in the relative importance of the different variables, I used a post-hoc Tukey test to identify which of the variables differed in their relative importance. This was done for the entire data set to identify if there was an overall difference in the relative importance of the four variables, as well as for the latitudinal subsets (described above) to see if the variable importance differed across the different latitudinal bands.

2.4 Results

Top variable combinations

Overall, the four-variable combination: temperature seasonality (BIO4), maximum temperature of the warmest period (BIO5), annual total precipitation (BIO12) and precipitation seasonality (BIO15) and performed best most frequently and was among the top 5 models for 75% of the species (Figure 2.3).

This was true for species breeding at all latitudes, though for species at high latitudes in the southern hemisphere (below -23.5°) the difference between this variable combination and the second best combination (with only three variables: the temperature seasonality, maximum temperature of the warmest period and precipitation seasonality) was smaller. Both combinations were in the top three models equally often; i.e. for our southern hemisphere high latitudes species total precipitation was less frequently important in describing species ranges (Figure 2.4).

The fit of models (using AUC on independent blocks) of the top variable combinations for the individual species were very similar (Figure 2.5). Models based on the three top variable combinations (BIO4+BIO5+BIO12+BIO15, BIO4+BIO5+BIO15+BIO18 and BIO4+BIO5+BIO18+BIO19; variable acronyms as in Table 2.1), result in AUC values >0.8 for 80% of the modelled species.

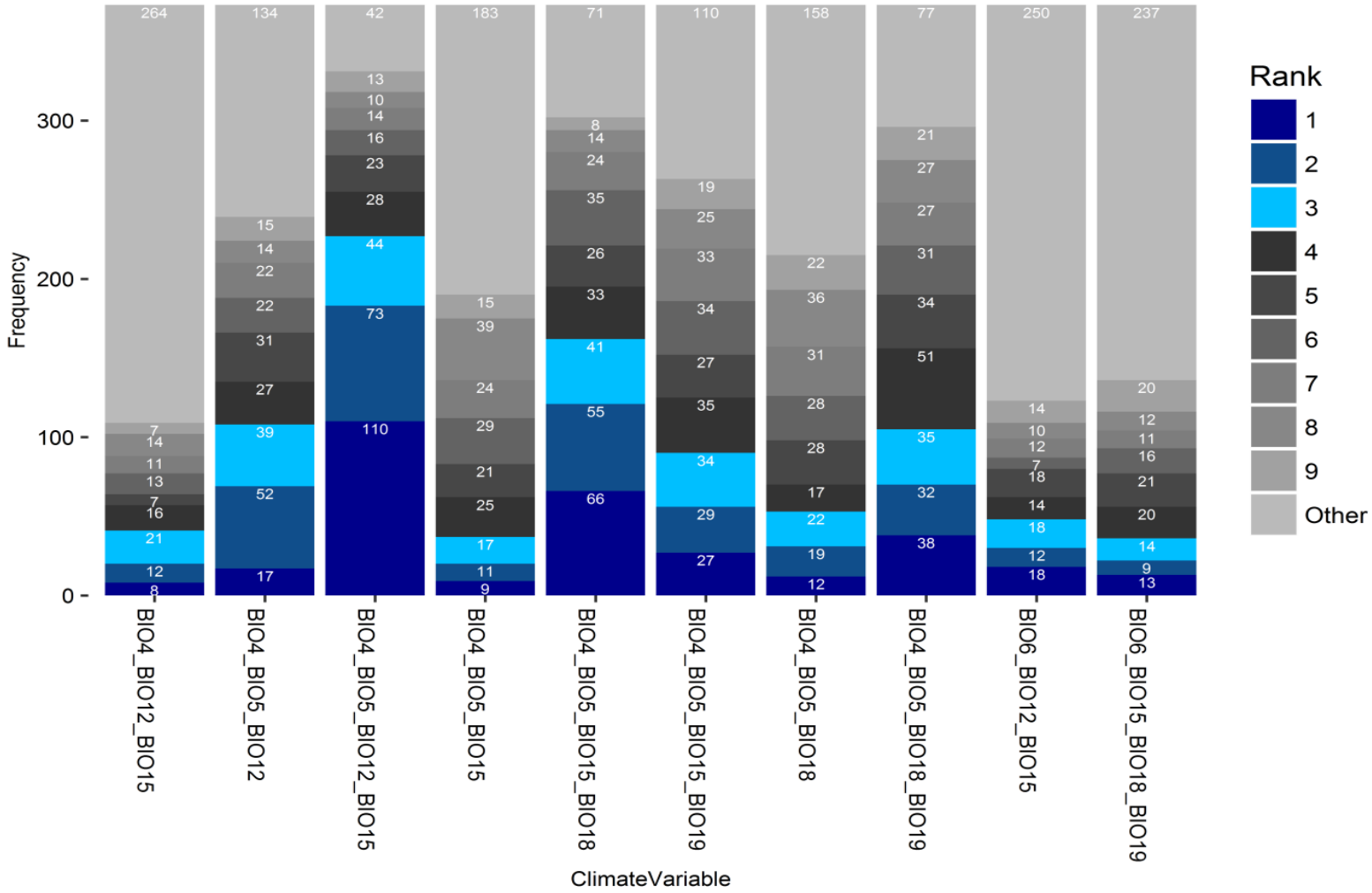


Figure 2.3: The ranked performance (based on AUC) of models built using different subsets of bioclimatic variables across the 400 species modelled. The Y axis indicated the frequency with which a particular variable combination was ranked as the top (Rank =1), second best (rank=2) etc. fitting model across the 400 species (blue shades = selected as one of the top three model combinations). Variable codes are described in Table 2.2. Results are shown for the ten top performing variable combinations (See Supplementary material, Figure S1 for all combinations).

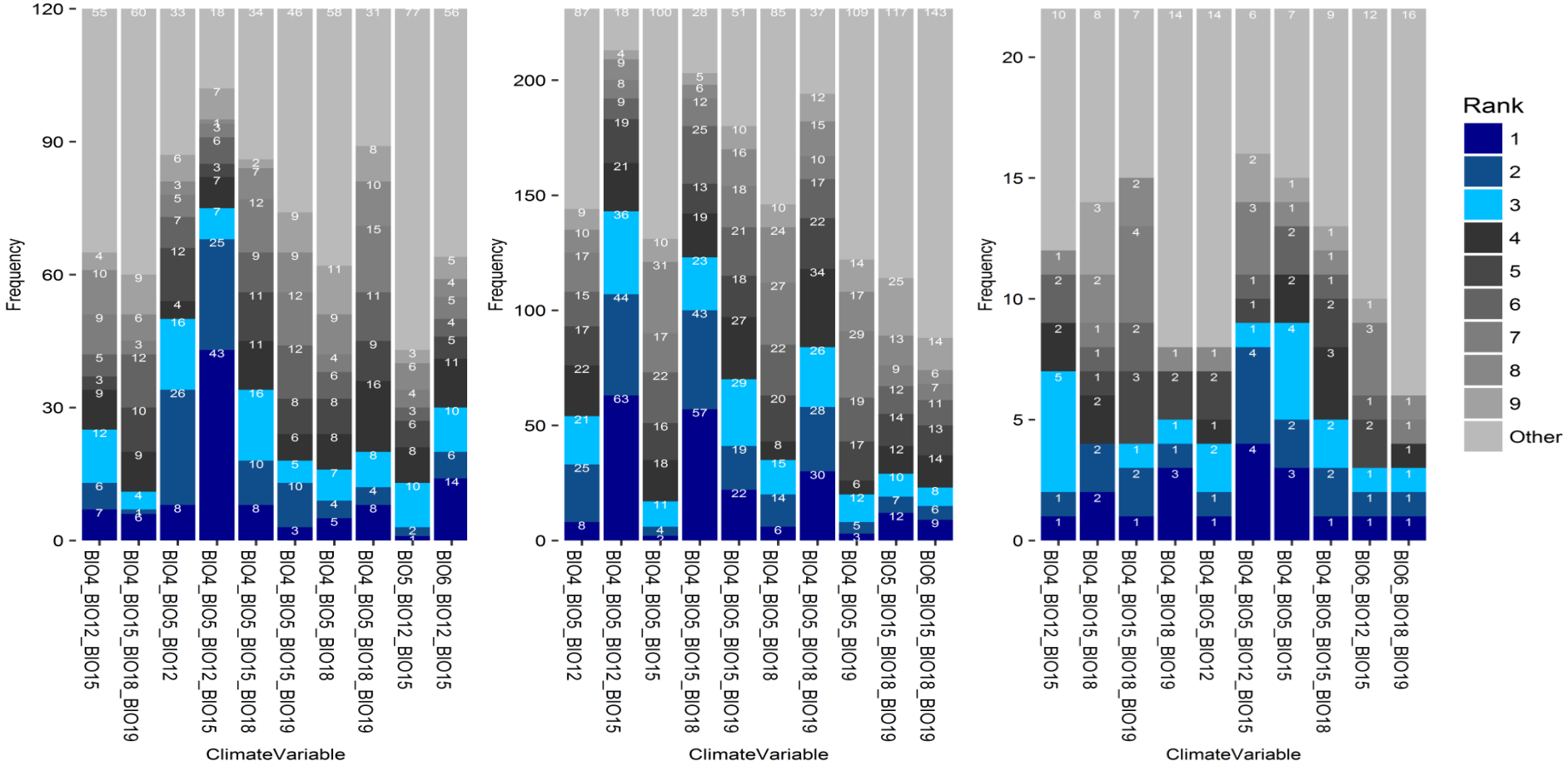


Figure 2.4: The ranked performance (based on AUC) of models built using different subsets of bioclimatic variables across the 400 modelled species, split by the latitude band a species occurs in. The Y axis indicated the frequency with which a particular variable combination was ranked as the top (Rank =1), second best (rank=2) etc. fitting model across the 400 species (blue shades = selected as one of the top three model combinations). From left to right they show variable ranking for species with a centre point at high northern latitudes (>23.5°), low latitudes (<23.5° to > -23.5°) and high southern latitudes (< -23.5°). Note the different numbers of species (few in southern hemisphere high latitudes) in these regions results in different y-axes for the three plots.

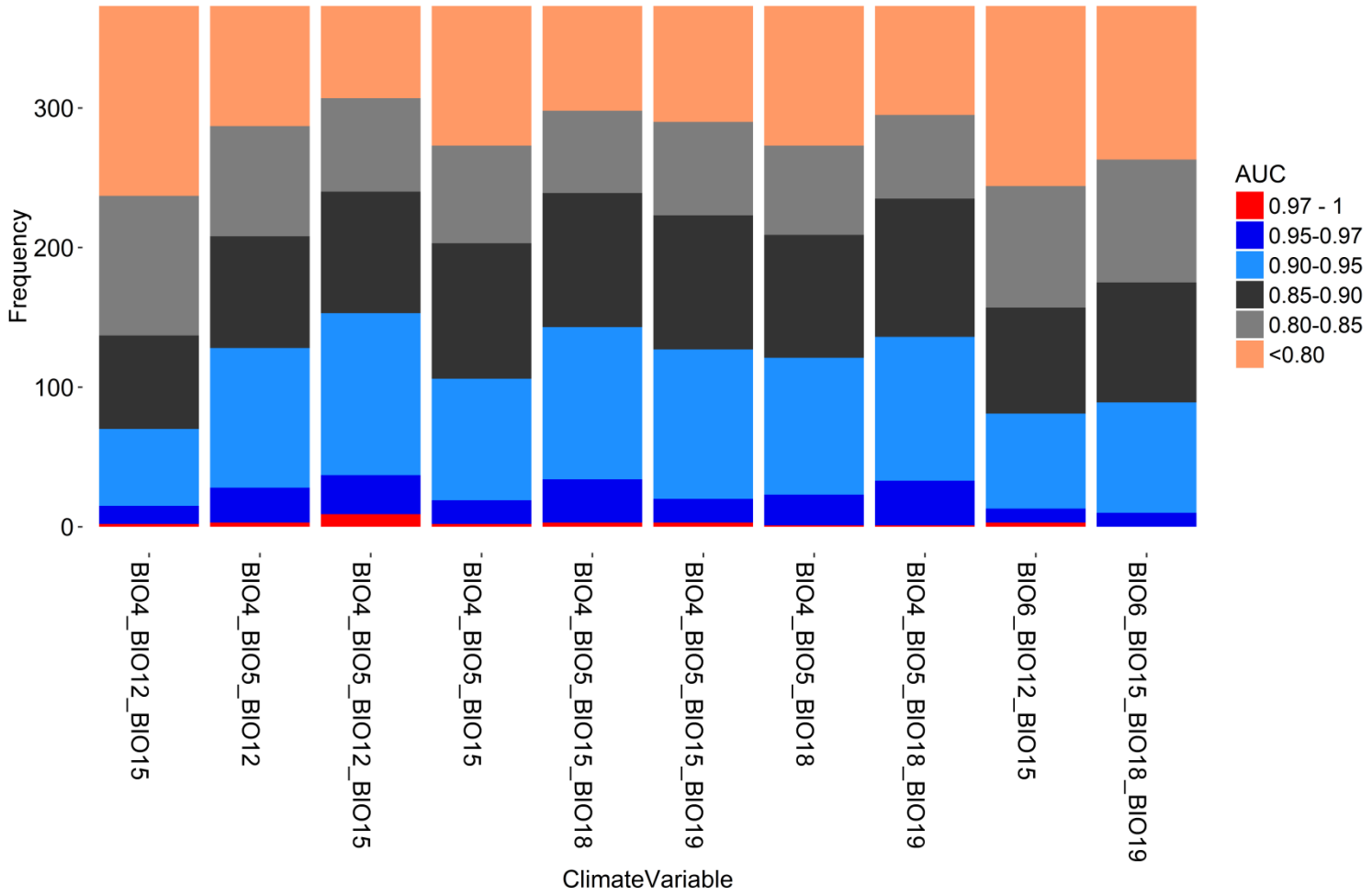


Figure 2.5: The frequency with which models built using the different variable combinations fell into different bands of model fit (based on AUC). Blue and red shades indicate very high AUC values (>0.90), grey indicating intermediate AUC values (<0.90 >0.80).

Variable importance for the top combination

For the top performing variable combination 'BIO4+BIO5+BIO12+BIO15', the variables differed significantly in their importance (ANOVA, $F_{(3,1487)} = 59.55$, $p < 0.001$). The variable 'maximum temperature of the warmest period' (BIO5) appears to contribute most to model performance (Post hoc Tukey, $p < 0.001$, between all variable combinations), typically increasing AUC by 0.05 when added to 3-variable models (Figure 2.6, Table 2.3). The importance of BIO5 is similar, though slightly higher, for species of higher northern latitudes (>23.5°) (ANOVA, $F_{(3,936)} = 94.77$, $p < 0.001$, Post hoc Tukey, $p < 0.001$). For species of lower latitudes and also those of high southern latitudes, of temperature seasonality (BIO4) is the most influential variable when added to models, increasing AUC by 0.45-0.5. Typically, when added to 3-variable models the most influential precipitation variables add only about 60% of the additional predictive power of the most influential temperature variables (e.g. gains of 0.03 vs 0.048 AUC units for the best precipitation vs the best temperature variable across all 400 species; Figure 2.7).

Table 2.3: Mean increase in AUC when adding the fourth variable to the three variable model, for each of the tested bioclimatic variables across all models. Red indicates temperature variables, blue indicates precipitation variables. Bold highlight the most influential variables across each row. High latitude > 23.5°, medium latitude < 23.5° and > -23.5°, low latitude < -23.5°.

	BIO4	**BIO5**	**BIO6**	**BIO12**	**BIO15**	**BIO18**	**BIO19**
All 400 species	0.040	**0.048**	-	0.030	0.015	0.026	0.012
Higher northern lats. (n = 257)	0.035	**0.060**	-	0.020	0.015	0.022	0.010
Lower lats. (n=94)	**0.050**	0.023	-	0.030	0.014	0.024	0.010
Higher southern lats (n=22)	**0.045**	0.013	-	-	0.013	0.020	0.01

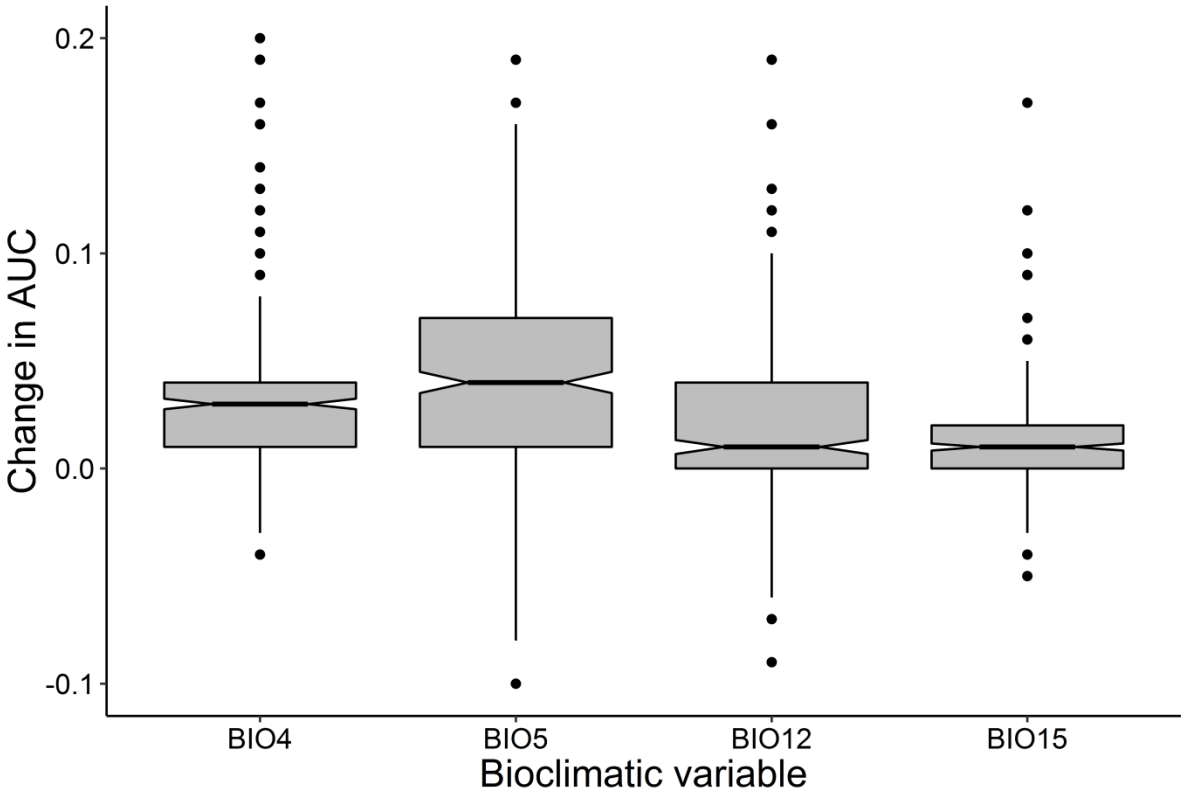
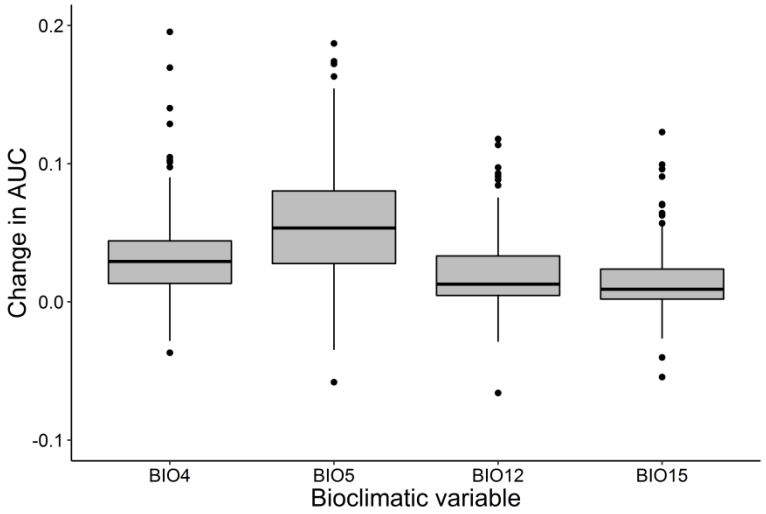
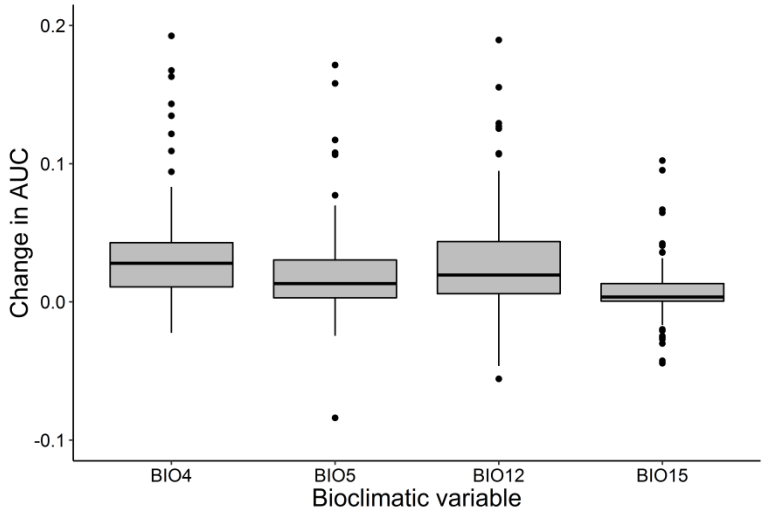


Figure 2.6: The variable importance (as measured by ΔAUC, when they are added to 3-variable models without them) of the individual variables that comprise the best 4-variable combination across all species.





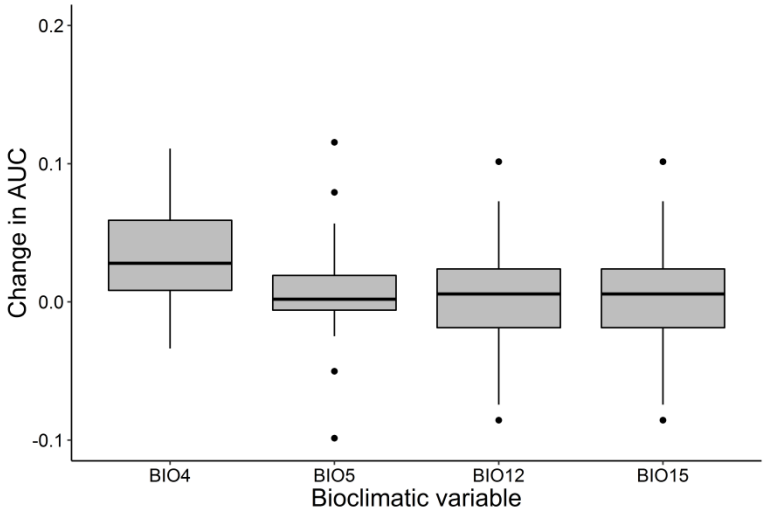


Figure 2.7: The variable importance of the chosen best variable combination across different latitudes. The top left figure shows the variable importance for species whose range centroid is located at a high latitude (>23.5°, n=235), the top right figure shows the variable importance for species with their range centroid in the tropical belt (<23.5° and >-23.5°, n= 116) and the bottom figure shows the variable importance for species with their range centroid at low latitudes (>-23.5°, n=22).

2.5 Discussion

The selection of predictor variables is a fundamental step when developing species distribution models (SDMs) to predict species ranges (Guisan & Zimmermann, 2000; Heikkinen *et al.*, 2006) and the importance of choosing ecologically relevant variables has been recognized previously (Araújo & Guisan, 2006). Selecting the most appropriate bioclimatic variables for all terrestrial bird species, based on ecological theory, is not possible with the data currently available. Model selection approaches have been suggested as a means to identify the most suitable variable to predict a species' range, when hand-selecting variables based on theory is not an option (Franklin, 2009). However, to do this individually for each of the world's birds (10,500 species) would be too computationally intense to implement. Here, I adopt an intermediate approach to explore the best variables combinations to use for such global modelling of species. I use prior ecological knowledge to inform the overall candidate variable subset, and then using model selection to explore whether common variable subsets work well for all species, or whether regional, latitudinal or ecological subsets of species require different bioclimatic predictors to describe their ranges.

The preselection of bioclimatic variables was based on the frequency with which they have been used previously, and successfully, across a broad variety of SDM studies. Of the 7 pre-selected variables (temperature seasonality, maximum temperature of the warmest period, minimum temperature of the coldest period, annual precipitation, precipitation seasonality, precipitation of the warmest quarter and precipitation of the coldest quarter), I derived all possible variable combinations under consideration of collinearity, and included all possible combinations of three (16) and four variables (7) for the analysis. Models with larger numbers of explanatory variables would have included collinear variables, or would have been vulnerable to overfitting. A variety of studies has successfully modelled species distribution with a lower number of predictor variables (Hole *et al*., 2009; Araujo *et al*., 2011; Bagchi *et al*., 2013; Baker *et al*., 2015). Additionally, the higher the number of explanatory variables in the model, the higher is the risk of overfitting (Randin *et al* 2006). Since the selected variable combination is intended to be used in a global study on all terrestrial birds, having a high number of predictive variables, could lead to additional modelling problems when birds with as few as 10 presences are included. Thus, the results in this chapter answer the question, which bioclimatic variables perform well across a large range of birds (including all kinds of range sizes) using a relatively low number of predictor variables, rather than exploring the ideal number of predictor variables included within a model.

For the majority of these species the predictor combination comprising 'temperature seasonality', 'maximum temperature of the warmest period', 'annual total precipitation' and 'precipitation seasonality', was among the highest performing models, suggesting that a single common subset of

bioclimatic variables performed well globally. Several of the alternative, but often closely related, variable combinations often also produced high model performance (based on AUC). When looking at subsets of the 400 species for higher northern (>23.5°) and lower latitudes (23.5° to -23.5°) this variable combination was the best performing combination. However at higher southern latitudes (< -23.5°) the variable combination 'temperature seasonality', 'max temp of the warmest month' and 'precipitation seasonality' (i.e. without 'total precipitation') performed equally well. However, the sample size for higher southern latitude species annual total precipitation was small (n=22, a consequence of the relatively small land area of the southern hemisphere below the Tropic of Capricorn). Generally there was not much difference in mean AUC scores amongst the top performing model combinations. For models built using the three best performing variable combinations, more than 80% of the models for species had an AUC above 0.8 and more than 40% had an AUC higher than 0.9.

Although I was able to identify a variable combination that performed well across the selected subset of species, the predicted distributions based on the chosen combination need to be treated with care. Using different predictor variables to model a species distribution can lead to very different predictions, especially when predicting into novel space (Araújo *et al.*, 2005a). Even similar high performing variable combinations can lead to different, sometimes even contradicting, predictions (Synes & Osborne, 2011; Braunisch *et al.*, 2013). Ideally, I would use several well performing variable combinations and explore the uncertainty around the projections that is introduced by using different variable combinations.

When working with a large set of species, the chosen best variable combination may not be among the top variable combination for all species. Although I found that the best variable combination generally had a high AUC score, for 12 % of the tested species this combination was not among the top five models. Thus, for those species, their range limits might be better described by using a different combination. If I used a true model selection approach to select the most parsimonious variable subsets, I would have assessed model fit using AIC, and non-nested models within 6 **Δ**AIC points of the best model would be ranked equally highly (Richards et al 2011). However, automating the exclusion of nested models and building models based on all variable combinations when modelling 10.500 species would be too computationally demanding to undertake here.

Overall, 'maximum temperature of the warmest period' was most the important bioclimatic variable within the chosen variable combinations, in terms of improving model fit of 3-variable models. Both temperature variables were of greater importance than the two precipitation variables, when

looking at the overall variable importance across all species. This was similar for higher latitudes, whereas for medium latitudes differences in variable importance were less pronounced.

The bioclimatic variables represent two primary properties of climate – energy and water. My results for the variable importance when looking at the different latitudinal bands are consistent with earlier studies on variable importance, which found temperature variables to be more important at northern latitudes and variables quantifying moisture availability to be more important at medium latitudes (Howard et al 2015). This change in variable importance is consistent with the species-energy hypothesis (Wright, 1983). In cold areas (towards the poles) energy (temperature) is the limiting factor of a species range, whereas in hot areas moisture availability is the limiting factor (Hawkins *et al.*, 2003).

Chapter 3

Global assessment of range changes of the world's terrestrial bird species under future climate change

3.1 Abstract

Species range changes under climate change have been widely documented. Movements towards higher latitudes and altitudes have been shown across a variety of species and taxa. These range changes not only result in reduced range extent between current and future species ranges but can also lead to a reshuffling of species community compositions, and the emergence of novel communities. Here, I highlight species and areas that are particularly threatened by climate change and require conservation intervention most urgently.

I use species distribution models (SDMs) to assess the potential impact of future climate change on the ranges of the world's terrestrial birds. I incorporate species dispersal abilities to produce realistic predictions of species range shifts. I summarize predicted changes in richness patterns as well as summarizing changes in range extent and overlap for individual species. I highlight species most at risk from climate change as well as areas where changes in the geographic distribution of species are most severe. Additionally, I define current avian communities across the different biological realms of the world, based on projected current species distributions and compare these to future community patterns.

I predict the highest changes in species richness in the Amazon basin, Eastern Africa and the Himalayas. These results parallel those simulated for other taxa by previous regional studies in these areas. Species that are projected to be most affected by future climate change are those with a restricted range or that occur at high latitudes and altitudes. Species turnover is highest in the Amazon basin, across the European Mediterranean and in the northern Nearctic and Palearctic regions. Localities of marked predicted shifts in avian communities to some extent mirror sites of highest turnover, with novel communities appearing mainly in the Amazon basin, across the European Mediterranean and in the northern Palearctic.

3.2 Introduction

Climate change is a major threat to global biodiversity (Thomas *et al.*, 2004), and impacts on species ranges are already evident across a wide array of taxa (Parmesan & Yohe, 2003; Chen *et al.*, 2011). A primary response of animal and plant species to climate change are shifts in their distribution (Parmesan, 2006), leading to a global reshuffling of species assemblages (Walther *et al.*, 2002; Root *et al.*, 2003). Some species are tracking suitable climate to higher latitudes and altitudes (Grabherr *et al.*, 1994; Easterling *et al.*, 2000a; Hughes, 2000; Kelly & Goulden, 2008), but idiosyncratic range shifts are also occurring (VanDerWal *et al.*, 2013; Gillings *et al.*, 2015) with some species even shifting their ranges to lower elevations (Tingley *et al.*, 2012; Gibson-Reinemer & Rahel, 2015). Hence, species are demonstrating individualistic responses, based on their abiotic tolerances, dispersal abilities and interactions with other species (Davis *et al.*, 1998; Guisan & Thuiller, 2005; Jeschke & Strayer, 2008b). Overall these range shifts can lead to changes in community compositions and the emergence of novel communities (Roy *et al.*, 1996; Williams *et al.*, 2007). Changing community compositions, attributed to climate change, have already been observed throughout the last century (Moritz *et al.*, 2008; Davey *et al.*, 2013) and will become more likely (Stralberg *et al.*, 2009). These changes can lead to novel interactions and imply additional threats for species (Gilman *et al.*, 2010; Lurgi *et al.*, 2012). Thus it is important to identify areas where changes in community compositions are likely to occur.

Contractions of species ranges under climate change have been found across a variety of taxa (Hill *et al.*, 2002; Wilson *et al.*, 2005; Svenning & Skov, 2006; Thomas *et al.*, 2006). Range contractions are predicted to be especially severe for endemic species in biodiversity hotspots (Malcolm *et al.*, 2006a) and for montane species (Sekercioglu *et al.*, 2008; La Sorte & Jetz, 2010). Identifying areas and species that are at threat from climate change through range losses and changes is important for the conservation of biodiversity (Thuiller *et al.*, 2005b). A better understanding of species potential future distributions can support conservation planning; for example, directing the locations of new protected areas or corridors (Hannah, 2008; Hagerman & Chan, 2009).

Birds are a well-studied taxon with a lot of available data and, consequently, a wide array of studies has addressed potential impacts of climate change. Changes in bird ranges under climate change have been assessed for individual species (Marini *et al.*, 2010), for assemblages within countries (Peterson *et al.*, 2002) and at sub-continental scales (Hole *et al.*, 2009; Lawler *et al.*, 2009; Barbet-Massin *et al.*, 2012a; VanDerWal *et al.*, 2013; National Audubon Society, 2015) using species distribution models (SDMs). At a global scale, current species ranges have been intersected with future climate and land-use scenarios to assess potential impacts on species ranges (Jetz *et al.*, 2007). The ranges of many birds are projected to contract significantly under climate change, as

many as 20% of the world's birds potentially being imperiled by land use and climate change (Jetz *et al.*, 2007). Consistent with other taxa, birds have, in recent decades, extended their ranges northward (Thomas & Lennon, 1999) and to higher latitudes (Pounds *et al.*, 1999). But there is also evidence that some species are unable to track their climate envelope rapidly enough to track changes in the location of suitable climate (Devictor *et al.*, 2008). Species with poor dispersal abilities are particularly prone to being more severely affected by dispersal lags (IUCN, 2009; Foden *et al.*, 2013). To date, the incorporation of dispersal abilities into species in distribution models has been uncommon, leading to widespread criticism (Berg *et al.*, 2010; Travis *et al.*, 2013). Comparing two basic assumptions of dispersal, full dispersal and no dispersal, suggests that, inclusion of dispersal data into SDMs can have substantial impacts on predicted distributions (Araújo *et al.*, 2006; Thuiller *et al.*, 2006). Recent approaches to predict future species distributions have introduced SDMs that incorporate dispersal (Génard & Lescourret, 2013). Further refinements to projections have also incorporated population and habitat dynamics (Franklin, 2010). These approaches should result in more realistic future predictions but are computationally intensive when considering large assemblages of species.

Here I project the impact of climate change on ranges and distributions of all terrestrial bird species globally for which robust SDMs can be created. I project range changes for more than 9,000 terrestrial bird species (Figure 3.1) under different climate change scenarios. I include biological traits (dispersal) for all the species, for the first time in a global study, to produce more realistic projections than have been made previously. The aim of this chapter is to assess the impact of climate change on terrestrial bird distributions at a global scale and to highlight those species and areas particularly at risk from climate change, and hence which most urgently require conservation intervention. In particular I will answer the following questions:

1. How is global avian richness projected to change as a consequence of future climate change?
    a. How do current and projected future patterns species of richness differ?
    b. How are future projections altered by additionally considering species-specific dispersal ability?
2. How are species' current ranges projected to alter under future climate change?
    a. What are the changes in range extent, range shift current and to what extent do current and future projected ranges overlap for individual species?
    b. In which areas of the world will future climate change have the greatest impact on species ranges?

3. How might different subsets of species affected by projected future climate change?
    a. Are montane species more robust to climate change than lowland species? Are the ranges of montane species projected to shift less than lowland species?
    b. Are wide ranging species less susceptible to reduced range overlap between current and projected future range extents?
4. How might avian community assemblages be reorganized as a result of projected climate change?
    a. What are the projections of species turnover as a result of future climate change across the world?
    b. Can we identify distinct avian communities at present and, if so, to what extent will these shift, either in range or in composition in future? Will climate change lead to novel avian communities forming?

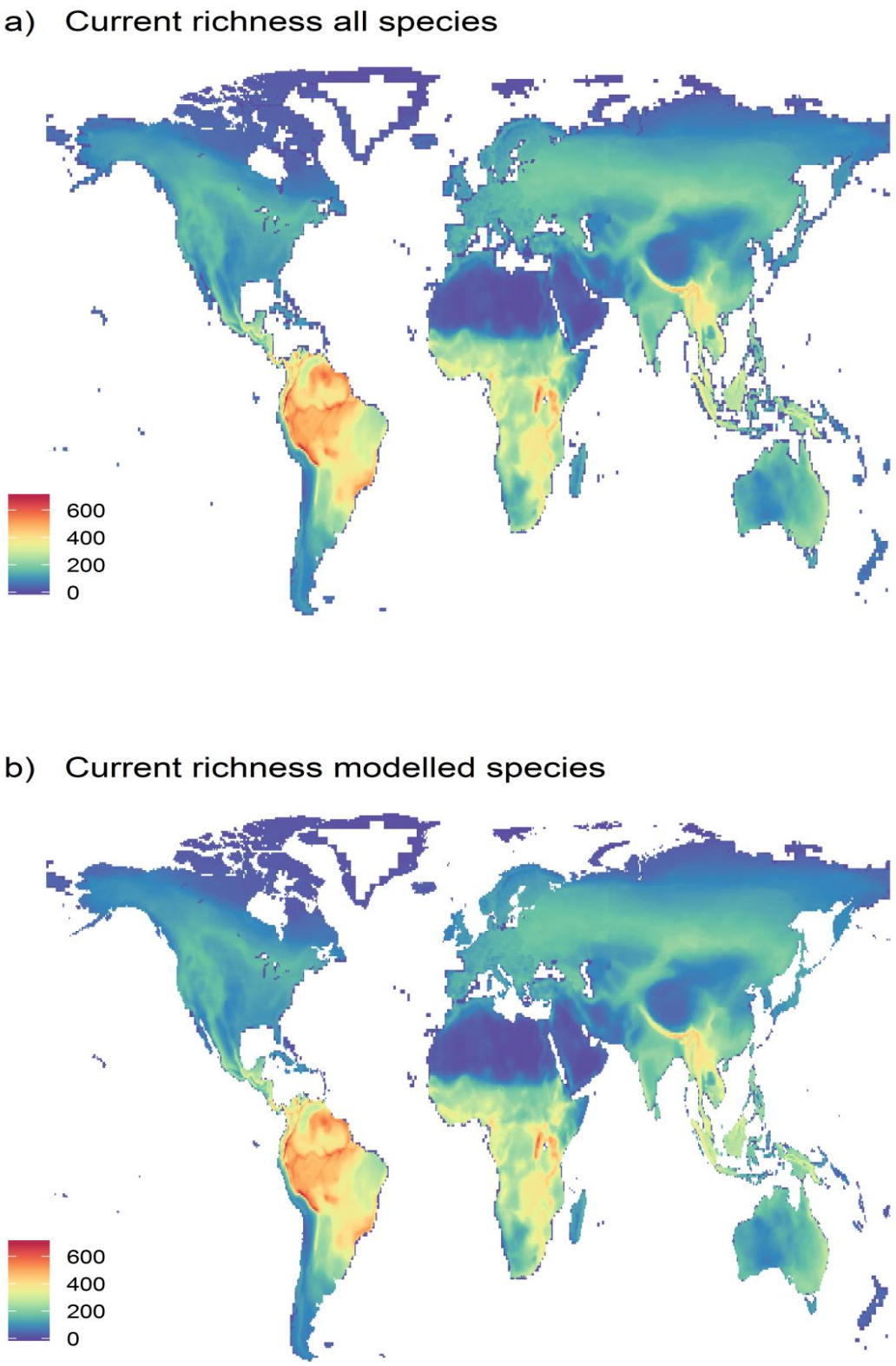


Figure 3.1: The graph shows the global species richness for: (a) all 10,178 bird species (b) for the species (9,196) with sufficient data to be modeled within this chapter. Richness is derived from individual species' breeding range polygons from BirdLife International (BirdLife International & NatureServe, 2012).

3.3 Methods

3.3.1 Species distribution data

I obtained global breeding range polygons from BirdLife International for 9,237 bird species (BirdLife International & NatureServe, 2012). For modelling purposes, the distribution data were gridded onto a 0.5° (lat-long) grid (55 x 55 km at the equator). Species were considered present in a cell if their polygon overlapped with at least 10% of a grid cell. Species whose breeding range intersected with fewer than 50 0.5° grid-cells were re-gridded onto a 0.25° grid, without the application of a minimum range overlap, i.e. any cell overlap on the 0.25° grid was considered presence. 6,982 species occurred in >50 0.5° grid cells, with the remaining 2,255 species ranges (which included many range-restricted species of high conservation priority) gridded at 0.25° degree resolution. Subsequent modelling was undertaken at 0.5° resolution for the more widely distributed species and 0.25° resolution for the restricted-range species. Any species with a range <10 grid cells at this finer resolution (705 species) were not considered any further due to the difficulties in modelling sparse data. This included a number of species that occur only on small, remote Islands whose ranges are likely to be not solely climate restricted (Schwartz *et al.*, 2006; Thomas, 2010). Seabird species (355 species) were excluded from the analysis due to the terrestrial focus of the study, and the fact that their terrestrial breeding localities are, to a large extent, dictated by factors other than terrestrial climate.

For modelling purposes, I selected pseudo-absence data for each species using a distance-weighted approach, following the method described in Chapter 2. I used an equal number of presences and absences to build models for each species. However, for species with a range <1000 cells at the relevant grid resolution for that species, I selected 1000 pseudo-absence points for the species. For each species, I produced five pseudo-absence datasets to be used in the species distribution models (SDMs).

3.3.2 Climate data

Contemporary climate: The bioclimatic data were obtained from WorldClim, and the same combination of four bioclimatic variables as selected in the preliminary analysis in Chapter 2, where used for characterising the species' ranges (Table 3.1).

Table 3.1: Bioclimatic variables used for the species distribution models.

WorldClim code	Variable name
BIO4	Temperature seasonality
BIO5	Maximum temperature of the warmest period
BIO12	Annual precipitation
BIO15	Precipitation seasonality

Future climate: I used three global climate models (GCMs), available from WorldClim, as being representative of future projections of climate change: CCSM4, GFDL-CM3 and HadGEM2-ES. These were selected as they have been shown to perform well in representing climatic regimes across three widely separate parts of the world: The Americas, Europe and Asia (McSweeney et al., 2015). All other GCMs available on WorldClim were either incomplete or evaluated to not perform well for at least one of the three areas when downscaling (McSweeney et al., 2015).

For each of the three GCMs I considered three greenhouse gas emission scenarios, the representative concentration pathways rcp26, rcp45 and rcp85. These rcp pathways have been named according to their radiative forcing values in the year 2100, relative to the pre-industrial values (+2.6, +4.5, and +8.5 W/m^2) (van Vuuren *et al.*, 2011). I omitted the rcp65 pathway, since data for this pathway was not available for all of the three chosen GCMs. Climate data were extracted for two time periods, one centred around 2050 (average climate data for 2041 – 2060) and a second centred around 2070 (average for 2061 – 2080) and for the same bioclimatic variables as the contemporary climate data.

3.3.3 Species distribution models

I modelled the relationship between current species' distributions and the four bioclimatic variables using three modelling approaches: Generalized Linear Models (GLM), General Additive Models (GAM), and Random Forest Models (RF), following the methods of Bagchi *et al.* (2013). These models were chosen based on their performance in previous assessments (Araújo *et al.*, 2005b; Prasad *et al.*, 2006; Meynard & Quinn, 2007; Elith & Graham, 2009; Wenger & Olden, 2012) and to provide a contrast between parametric (GLM), semi-parametric (GAM) and machine learning (RF) methods (Bagchi *et al.*, 2013).

Spatial dependence

I dealt with spatial dependence using the blocking approach described in Chapter 2. The data were split into 10 blocks, using the world's ecoregions as subunits that were aggregated to form each block (see Bagchi et al. 2013 for details). Models were build based on 9 blocks and performance was assessed based on predictions to the left-out 10th block.

For some species with a restricted range, this blocking approach would not work (e.g. all records occur in one block). In such situations, I applied a 30:70 data splitting approach for model development and testing, though acknowledge that the resultant models are likely to be less robust than those produced using a blocking approach. I repeated the 70:30 splitting and pseudo-absence selection 10 times for modelling and testing. Note that, despite its shortcomings 70:30 data splitting is still the accepted norm in most SDM modelling.

Generalized linear models (GLM)

I used generalized linear models (McCullagh & Nelder, 1989) to fit relationships between the bioclimatic variables and species distributions. I allowed up to 3rd order polynomials for the four bioclimatic variables, resulting in 81 possible combinations. I fitted 81 models to nine of the blocks, leaving one block out at a time, and assessed model performance based on the left-out block each time. Using the mean AUC across the ten left out blocks, I chose the combination of polynomial degrees that maximised AUC. Since the pseudo-absences for each species were drawn from different extents, the relationship between the predictor and response variable varied. For some species, for some of the data subsets, this resulted in complete or quasi-complete separation for higher polynomials (one of the predictor variables being perfectly separated by the response variable (Albert & Anderson, 1984)). These combinations were not considered any further. The best combination of polynomials was used to fit a final set of ten models. The mean AUC across the left-out blocks of these models was used as an indicator of the models' fit.

General additive models (GAM)

I applied general additive models, using thin-plate regression splines (Wood, 2003; Wood, 2006) to model the relationship between species' occurrence and the four bioclimatic variables. I used the 'gam' function of the 'mgcv' R package, fitting a Bernoulli response, using a logit link (Wood, 2011; R Developement Core Team, 2012). I fitted models to the species data omitting one block at a time and used AUC to assess model performance based on the left-out blocks.

Random Forest models (RF)

I used random forests, a machine learning approach, to describe the relationship between the response variable and the predictors. I used cross-validation to define the two main parameters required for the model, the number of trees (ntree) and the number of predictors used to build each tree (mtry) (Prasad *et al.*, 2006). The number of predictors was set to be between one and three and the number of trees was set to initially 1000, which was incremented by 500 trees at a time. The model was built on nine blocks each time and assessed on the left-out tenth block using AUC. If a larger model improved the previous model by > 1%, it was accepted. This process was repeated until the AUC was not improved any further. The number of trees (ntree) and predictors (mtry) that had the best mean AUC across the ten left-out blocks were used to build the final set of models. The models were implemented using the 'randomForest' package in R (Liaw & Wiener, 2002; R Developement Core Team, 2012).

3.3.4 Predictions

Due to computational limitations, species potential ranges were not predicted to all global terrestrial cells but to a subset of the global grid that was within the colonisation potential of species. For species gridded to a 0.5° grid (i.e. more widely distributed species) I used the current distribution of a species with the terrestrial zoogeographic realms of Holt *et al.* (2013) to determine the extent to which the future distributions were projected for that species. These realms are often defined by unsurpassable biogeographical barriers for many species, and using realms to define the modelling extent is more biologically valid than the rather arbitrary political boundaries that are more often employed for SDM analyses. For each species, I projected to the biological realm that the species currently occurs in, as well as to any adjacent realms, that the species might be capable of colonising in future. Figure 3.2 shows the zoogeographic realms used and Table 3.2 the resulting neighbouring realms used for each realm of occurrence. If a species occurs currently in more than one realm, models were applied to all currently occupied realms as well as to all of the relevant neighbouring realms. For species of restricted range extent (i.e. those occurring in <50 half-degree cells), predictions were made to all areas within 1000 km radius of a species' current range. This 1000km buffer exceeded the maximum potential dispersal distance over the current century (117±157km, mean±SD) for the majority of these restricted-range species (based on estimated generation length, mean natal dispersal potential and the number of generations completed in the period (Equation 1 in next section); data from BirdLife (in prep.)). 450 projections of range extent were produced for each species in each future time period (5x Pseudo-absences, 10 x blocks, 3 x GCM, 3 x rcp), from which multi-model ensemble median projected changes (Thuiller, 2004; Araújo *et al.*, 2005a), and their variability, were estimated.

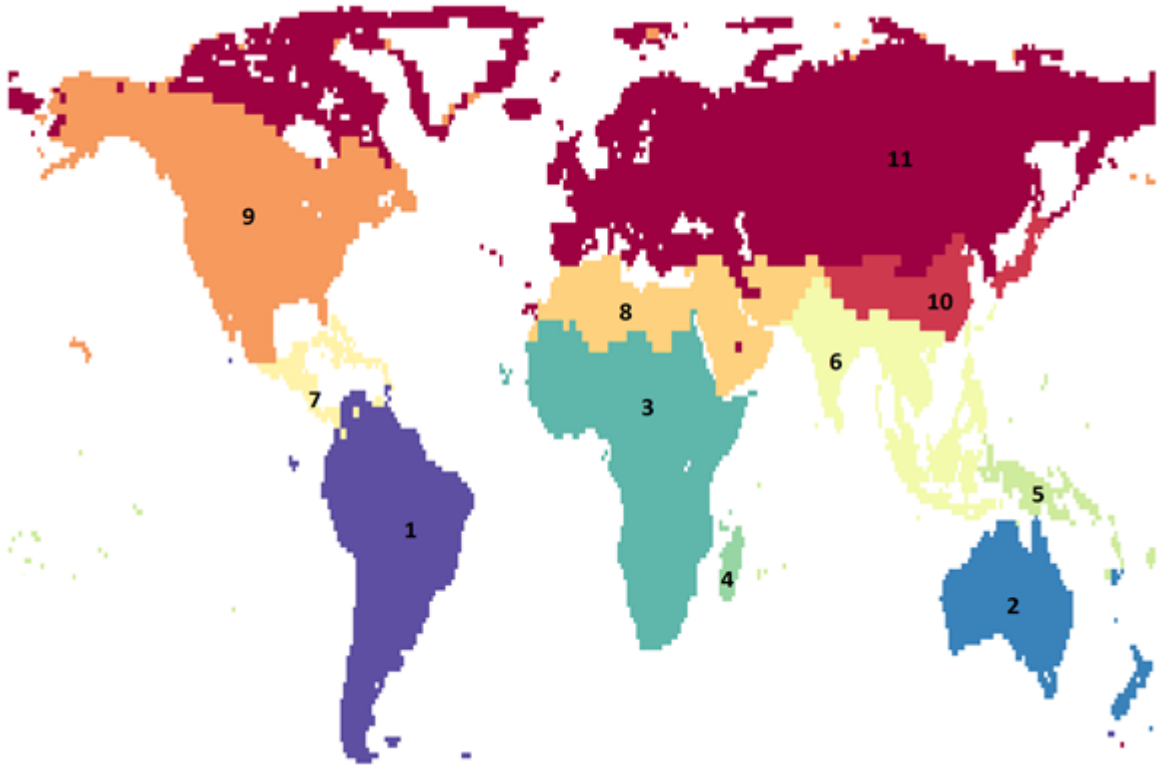


Figure 3.2: Map of the terrestrial zoogeographic realms by Holt et al. (2013). See Table 3.2 for realm definitions for numbered regions.

Table 3.2: The individual terrestrial zoogeographic realms and the neighbouring realms to which species' distributions were also projected. Realm numbers relate to the numbers in Figure 3.1.

Realm	**Realm number**	**Neighbouring realm I**	**Neighbouring realm II**	**Neighbouring realm III**	**Neighbouring realm IV**
Neotropical	**1**	7	-	-	-
Australian	**2**	5	6	-	-
Afrotropical	**3**	4	8	-	-
Madagascan	**4**	3	-	-	-
Oceanian	**5**	2	6	-	-
Oriental	**6**	2	5	8	10
Panamanian	**7**	1	9	-	-
Saharo - Arabian	**8**	3	11	-	-
Nearctic	**9**	7	11	-	-
Sino - Japanese	**10**	6	11	-	-
Palearctic	**11**	8	10	9	-

Thresholding climatic suitability values from models

To converting modelled suitability data from SDMs to projections of presence or absence for a species (which is often necessary for simplifying likely impact summaries), I followed the common practice (Freeman & Moisen, 2008; Franklin, 2009) of applying thresholds to convert projected continuous suitability values (or likelihood of occupancy) to binary data (i.e. projected suitable or unsuitable). Species-specific thresholds were used that optimized the fit of the resultant present-day suitability models to current observed distributions, using the kappa statistic (Cohen, 1960) to assess model fit.

Using natal dispersal data to project realistic range changes

To avoid predicting unrealistic increases in range, beyond a species dispersal capability, I limited projected range alterations based on species-specific trait data. I projected a species potential future range to only occur in areas of suitable climate that were within the distance *dx* of the current range edge of a species, using the following formula:

Eqn. 3.1:

$$dx = \left(\frac{projection\ period}{age\ at\ first\ breeding}\right) * natal\ dispersal\ distance$$

where the projection period is the duration (in years) between the contemporary modelled range and the future time period (2050 or 2070), the age at first breeding is the typical time (in years) between a species birth and first breeding and the natal dispersal distance of a species is the mean distance between the place of birth and the place of first breeding of a species (following e.g. (Baker *et al.*, 2015)). The dispersal data were made available from unpublished data (Joe Tobias, UCL) derived from the quantified relations between dispersal ability and wing biometric data. Data for the age at first breeding were obtained for most species from BirdLife International (in prep.), derived from published data. 909 species lacked data for age of first breeding in the BirdLife dataset; for these species the age of first breeding was either sourced from the primary literature (n = 37 species) or an estimate of the mean age of first breeding was derived based on closely related species (usually derived from species in the same genus). I restricted the dispersal ability for species endemic to islands since, in this situation, summing natal dispersal distance over a prolonged time interval does not necessarily reflect the ability of a species to travel a single long distances over water. If an island endemic species' natal dispersal distance was shorter than the distance to the nearest neighbouring island, but their summed dispersal ability (from Equation 2.1) was sufficient to cross, I restricted the total dispersal to 10x the natal dispersal distance. This allowed for the possibility that rare long distance dispersal events much longer (10x) the typical natal dispersal could

result in range expansion to more distant areas but not, for example, dispersal events of 50-70x the natal dispersal distance (for species that breed in the year following their birth).

Model performance

I used AUC to evaluate the performance of the species distribution models fitted to the present period. For each species, AUC values were calculated for the individual left-out blocks from the 10 fitted models and a mean AUC across these 10 validation blocks was calculated. I then compared the resultant AUC values across the different model types, using a one-way ANOVA, to test if there was a significant difference between the mean AUC values. I also tested for significant differences in model performance between species with small (<50 cells) and large (> 50 cells) ranges and between species assigned to different IUCN threat categories, using a Wilcoxon signed rank test for non-normal distributions and a one-way ANOVA respectively. Additionally, I checked for spatial patterning in model performance, calculating the mean AUC value of models for all species that occurred within a grid cell, based on their current range polygons. 41 species were excluded from further analysis because they had AUC values of < 0.7 for all three model types.

Projected range changes across different latitudes, altitudes and range sizes

I calculated changes in projected range extent and range overlap (between present modelled and projected future range), and the distance between current and future range centroids. I then checked whether there were systematic differences in these variables in relation to latitudinal altitudinal bands and in relation to current range extent. I used a Kruskal-Wallis test to assess if differences among groups were significant, and subsequently assessed which pairs of groups differed using post hoc tests (Kruskal-Wallis Nemeny) for pairwise comparisons.

Latitudinal bands were defined as high northern latitudes (> 60°), temperate northern latitudes (60° to40°), subtropical northern latitudes (40° to 23°), tropical latitudes north of the equator (23° to 0°), tropical latitudes south of the equator (0° to -23°), subtropical southern latitudes (-23° to -40°), and high southern latitudes (-40° to -60°). Ranges were split into several bands with species currently occurring in <50 cells, 50 to 500 cells, 500 to 1500 cells, 1500 to 2500 cells and > 2500 cells. Altitudinal bands were split in minimum altitude a species occurs at (< 500 m, 500m to 1000m, 1000m to 1500m, 1500m to 2000m and > 2000m), based on the minimum values of their altitudinal range. For this analysis 6218 species were included for which altitudinal range data was available from BirdLife (BirdLife International & NatureServe, 2012).

3.3.5 Species Turnover

To characterize the geographic pattern of changes in community composition, due to species changing ranges, I calculated the turnover within each grid cell until 2050. I extracted the current

and future projected species community for each grid cell and calculated the Bray-Curtis dissimilarity (Bray & Curtis, 1957). Projected climatic suitability for each species for this analysis was based on the ensemble median projections from the three SDMs types. Future projections for each species for this analysis were based on the mean suitability across the three GCMs (CCSM4, GFDL-CM3, HadGEM-2ES). For simplicity, in this chapter, these results are presented for only a single, medium emission RCP pathway (rcp45; for rcp26 and rcp85 see supplementary material S3). Turnover was based on simulations of species presence or absence in a cell, using thresholding as described previously.

3.3.6 Species community analysis

I used the same projections described above (of individual species occurrences within each terrestrial grid cells) to group cells in those containing similar avian communities based on their modelled species assemblages in a period. I derived species communities for grid cells for the present and the mid-term future period (i.e. 2050) only due to computational constraints, and due to the increased uncertainty in individual species projections over longer periods (e.g. (Baker *et al.*, 2015)). The global grid was split into the zoogeographic regions (Figure3.2, (Holt *et al.*, 2013)). The Palearctic was split into two halves for the analysis, due to computational limitations. The split was made along the Ural Mountains roughly following the geographic transition between Europe and Asia. I calculated the Bray-Curtis dissimilarity between each pair of cells within a biological realm. Subsequently I grouped the grid cells based on the Bray-Curtis dissimilarity matrix for each realm using a hierarchical agglomerative cluster analysis, based on Ward's criterion (Murtagh & Legendre, 2014) minimizing the within cluster variance, to define species communities (Stralberg *et al.*, 2009).

Since limited information exists regarding the broad-scale species assemblages within the zoogeographic regions, I used k-means cluster analysis to predetermine the number of communities within each realm. The k-means algorithm aims to find a partition at which the empirical mean of a cluster and the points within the cluster is minimized (Jain, 2010). I used the k-means function from the 'stats' package (R Developement Core Team, 2012), based on the k-means algorithm by (Hartigan & Wong, 1979). I tested different numbers of clusters, and chose the minimum number of clusters that explained 95% of the variance, calculated as:

Eqn. 3.2:

$$1 - \left(\frac{total\ within\_cluster\ sum\ of\ squares}{total\ sum\ of\ squares}\right)$$

I did this for all realms with the exception of the Saharo-Arabian, the selected number of clusters for this realm explained 90% of the variance (to explain 95% of the variance required the definition of many more communities than was biologically realistic).

I then grouped the cells of each realm into the chosen number of clusters. For the future communities, I identified for each grid cell within a biological realm, the most similar present day cell according to the Bray-Curtis dissimilarity matrix, I the assigned the future community based on the community of the matched present cell. The community analysis was carried out using the 'vegan' package in R (R Developement Core Team, 2012; Oksanen *et al.*, 2015).

3.4 Results

3.4.1 Model performance

I modelled the distribution of 9,196 terrestrial bird species (746 species were excluded due to low number of presences or low model performance, see Supplementary material S3, Figure S1). The overall model performance was high (mean AUC = 0.87, 0.87 and 0.98 for GAM, GLM & RF respectively), when predicting to the left out blocks (Figure 3.3). Overall, the RF models performed better than the GLM and GAM models.

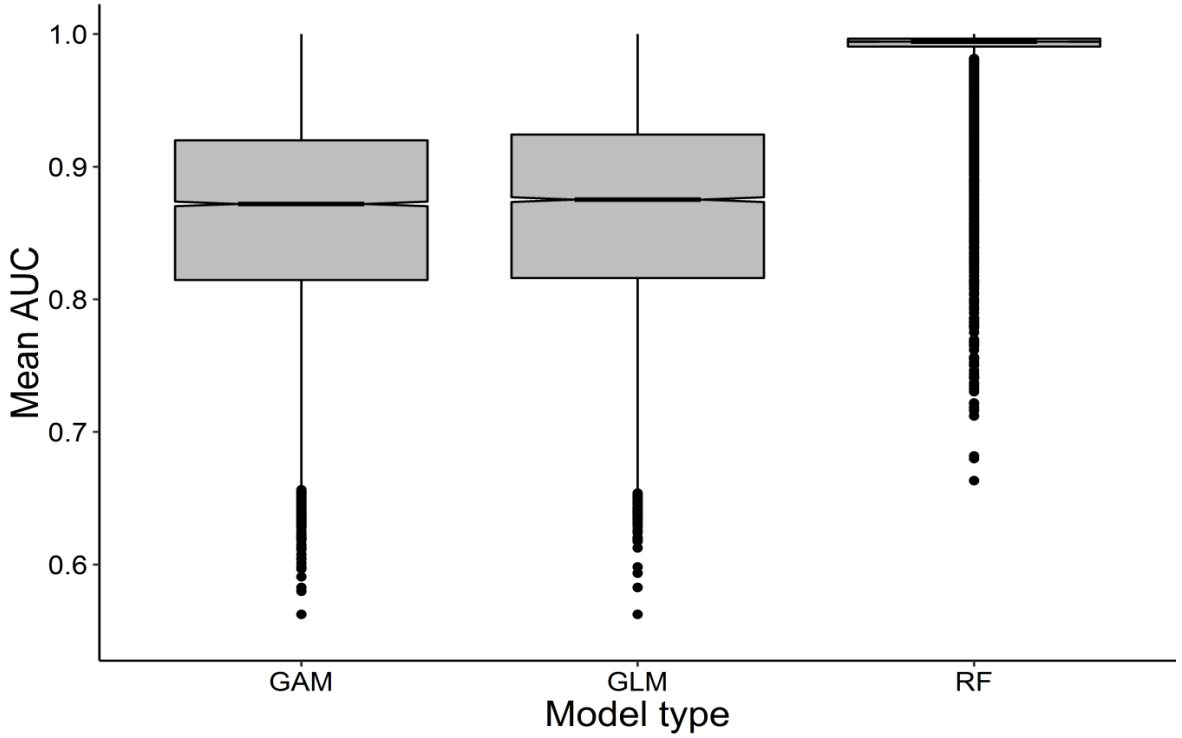


Figure 3.3: Mean AUC values across all species for the three SDM types (GAM, GLM and RF).

The AUC values are differed significantly for species assigned to differing IUCN threat categories with models for species classified as endangered (EN) performing significantly worse than models for species of other threat status (see supplementary material S3, Figure S3.2). There was no significant difference in model performance for species with small range (<50 cells) versus large (>50 cells) range extents (Wilcoxon Signed-Rank, W= 6986719, p = 0.1143), see Supplementary Material S3, Figure S3.3).

There was spatial patterning in the model performance, based on a global plot of the mean AUC of all species projected to occur within each grid cell, with a globally overall high performance but areas of lower performance scattered across the species poor areas of northern Africa and parts of the Palearctic. (see Supplementary Material, Figure S3.4).

3.4.2 Changes in global species richness patterns

For simplicity of presentation in the main body of this thesis chapter I present only results based on the middle-of-the-road rcp45 emission pathway and for the mid-century (2050) period. Predicted species richness patterns based on the other two emission pathways rcp26 and rcp85 and for the 2070 period are presented in the Supplementary Materials (S3; Figures S5 and S6). All results are based on the ensemble median values from the three model types (GAM), GLM & RF). All future predictions presented are ensemble means derived from the three General Circulation Models (GCMs) used unless specified differently.

The simulated, current global avian richness patterns (Figure 3.4a) match well with the observed richness patterns (Figure 3.1b). The pattern of future species richness (Figure 3.4b) is similar, in many areas, to that of current richness (Figure 3.4a), although overall richness is projected to decline. Amazonia, in Brazil, is projected to experience marked changes to species richness by 2050. In this region, richness remains high in bordering mountainous areas such as the Guyana Highlands, east of the northern range of the Andes and in the Brazilian Highlands, but richness in the Amazon basin is markedly lower in 2050 compared to present.

The projected future species richness (Figure 3.4) based on projections considering species' dispersal ability is markedly different to projections that assume species can reach all suitable areas, i.e. the latter being the more usual approach of assuming unlimited dispersal ability (Figure 3.5). For the remainder of this chapter all future projections are based on the more realistic projections of range change that incorporate the likelihood of dispersal to climatically suitable cells.

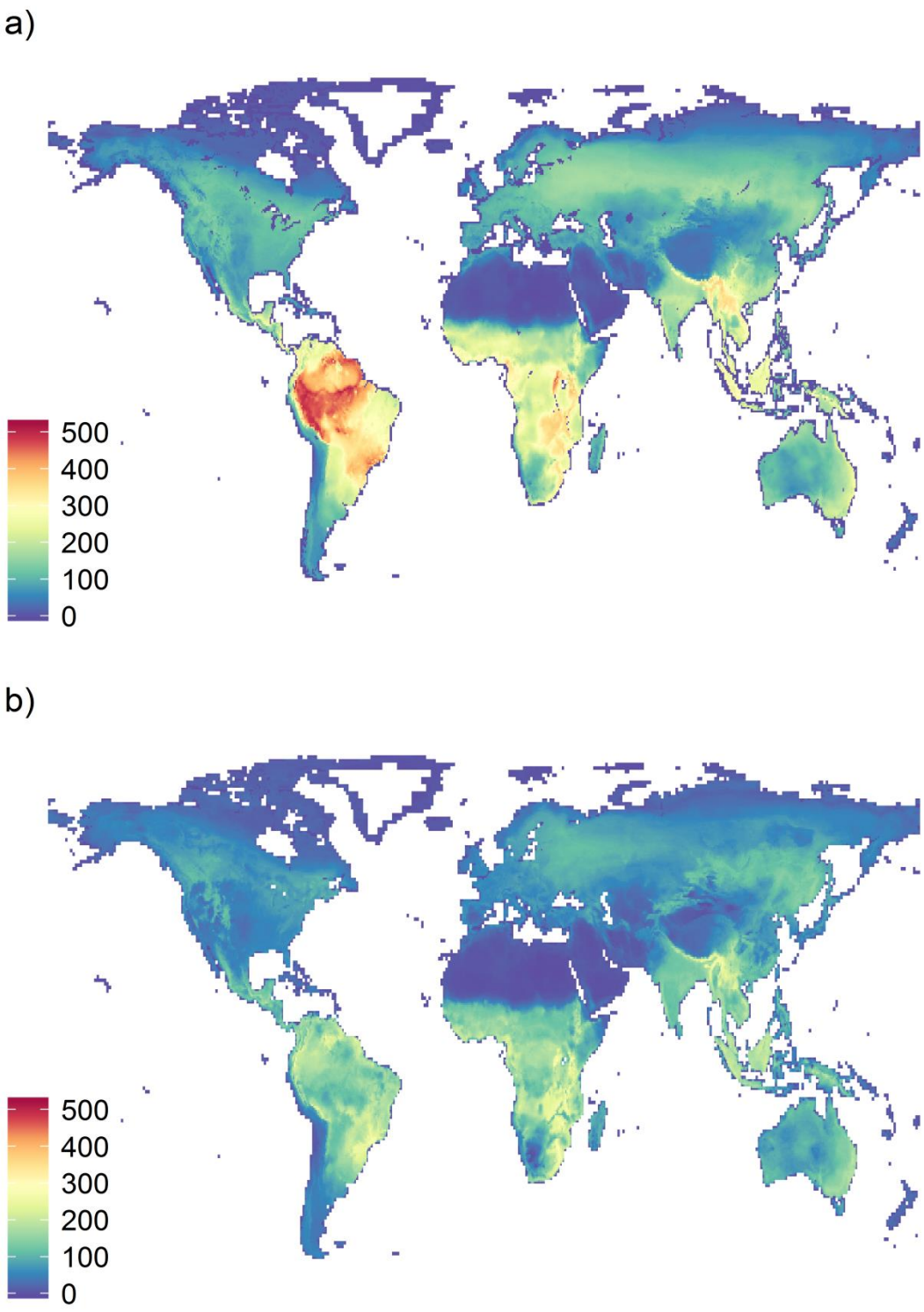


Figure 3.4: (a) Predicted species richness of modelled species (9,196) for the current period (1960-1990). (b) Predicted richness in 2050 under a medium emission scenario (rcp45), based on an ensemble across SDMs and GCMs.

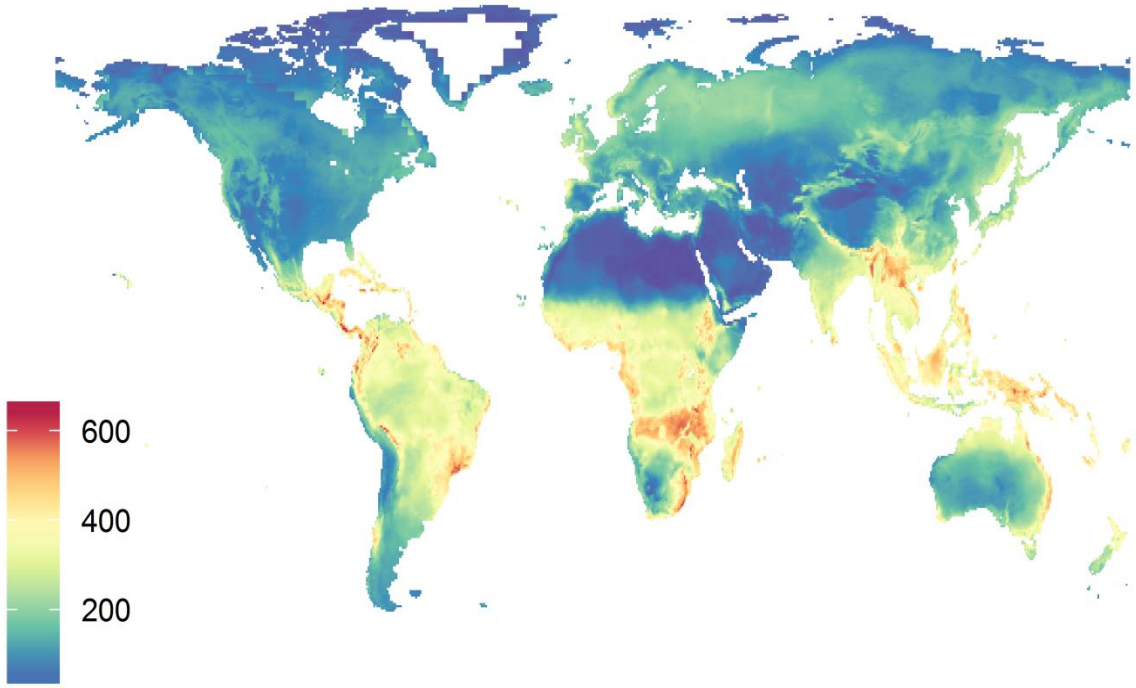


Figure 3.5: Predicted future species richness under a medium emission scenario (rcp45) by 2050 assuming unlimited dispersal ability of species.

3.4.3 Changes in range extent and overlap

Under the medium emission scenario (rcp45) 7,648 of the modelled terrestrial bird species are predicted to experience range changes (declines or increases) exceeding 10 percent of their current range by 2050, though predictions of range changes varied amongst the GCMs (Figure 3.6). Whereas the proportional range changes for species resulting from the CCSM4 and HadGEM-2ES GCMs are similar, the predictions based on future climates from the GFDL-CM3 GCM differed from these; the latter projecting future range losses to be more severe (Figure 3.6 a,d,g).

Based on the ensemble mean, 867 species were predicted to have no climatically suitably areas remaining within colonisation distance in the future. A further 993 species were predicted to have a future range >75% smaller that their current range and 1,149 species predicted to decline in extent by 50-75% (Figure 3.6, b,e,h). The majority of species predicted to experience significant range losses, including many species predicted to lose all their range, are located in the Amazon basin. Many species predicted to lose >50% of their range occur in eastern Africa and South-east Asia, with the Himalayan region in particular containing many such species (Figure 3.7; for the proportions of species with declining ranges see Figure S3.7).

Based on the ensemble mean across the 3 GCMs approximately 40% of the modelled species have <50% overlap between their current and future ranges. Of these species, 1,108 have <25% overlap and 951 species have no overlap between current and future ranges (867 with no climatically suitable area remaining and 84 with complete loss of range overlap; Figure 3.6, c,f,i). Spatially, areas with high projected species richness changes correlate with the areas having high numbers of species that are predicted to substantially decline in range extent, namely the Amazon basin, East Africa and the Albertine Rift and the Himalayas, as well as the Palearctic (Figure 3.8, for proportion of species with reduced range overlap see Figure S3.8).

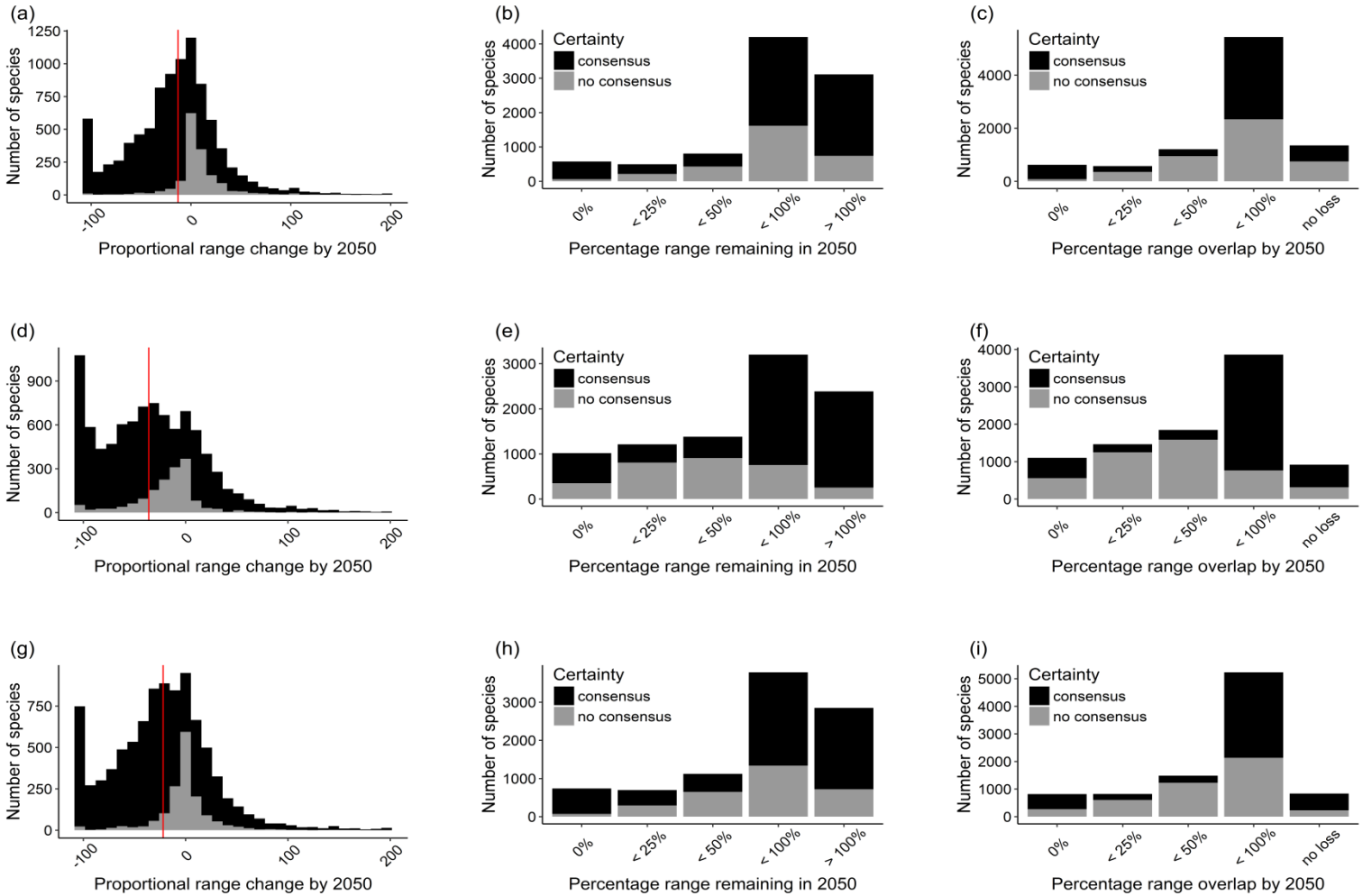


Figure 3.6: Mean proportional range change (a,d,g), percentage range remaining (b,e,h) and overlap of species ranges between their projected current and future (2050) ranges (c,f,i) under a medium emission pathway (rcp45). Projections are made using three different general climate models (GCMs) CCSM4 (a, b, c), GFDL-CM3 (d, e, f) and HadGEM-2ES (g, h, i). Black indicates that all three GCMs predict the same outcome for the species; grey shading indicates that there was no consensuses with the other two GCMs. Vertical, red lines indicate the median value. Note, on the bar charts the abbreviated footers are as follow: <25% = 1-24%, <50% = 25-49%, <100% = 50-99%, >100% = 100-∞%.

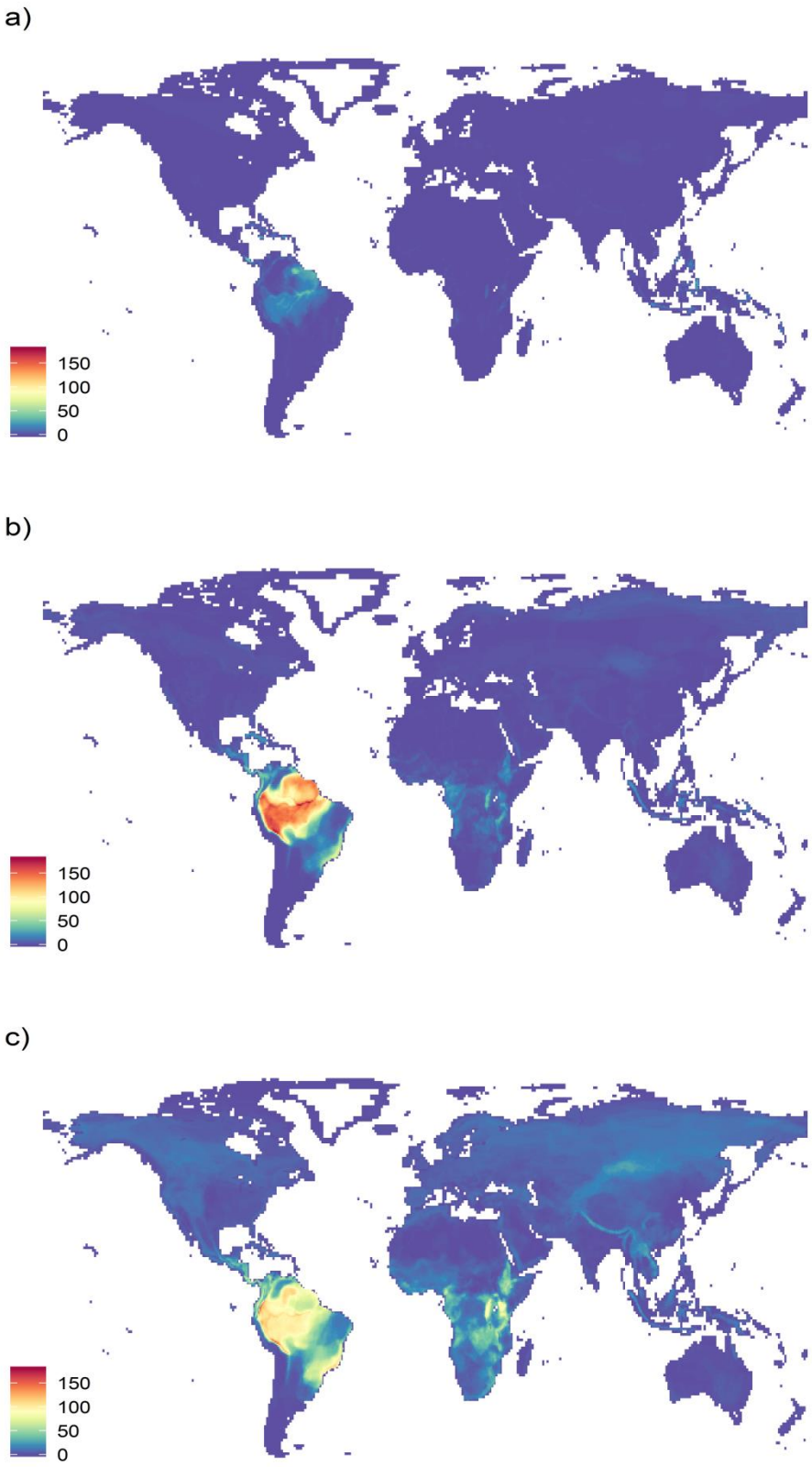


Figure 3.7: The current richness of species predicted to have the largest range declines under a medium emission scenario (rcp45) by 2050. (a) species predicted to be extinct by 2050, (b) species predicted to lose > 75% of their current range and (c) species predicted to lose between 50% and 75% of their current range extent.

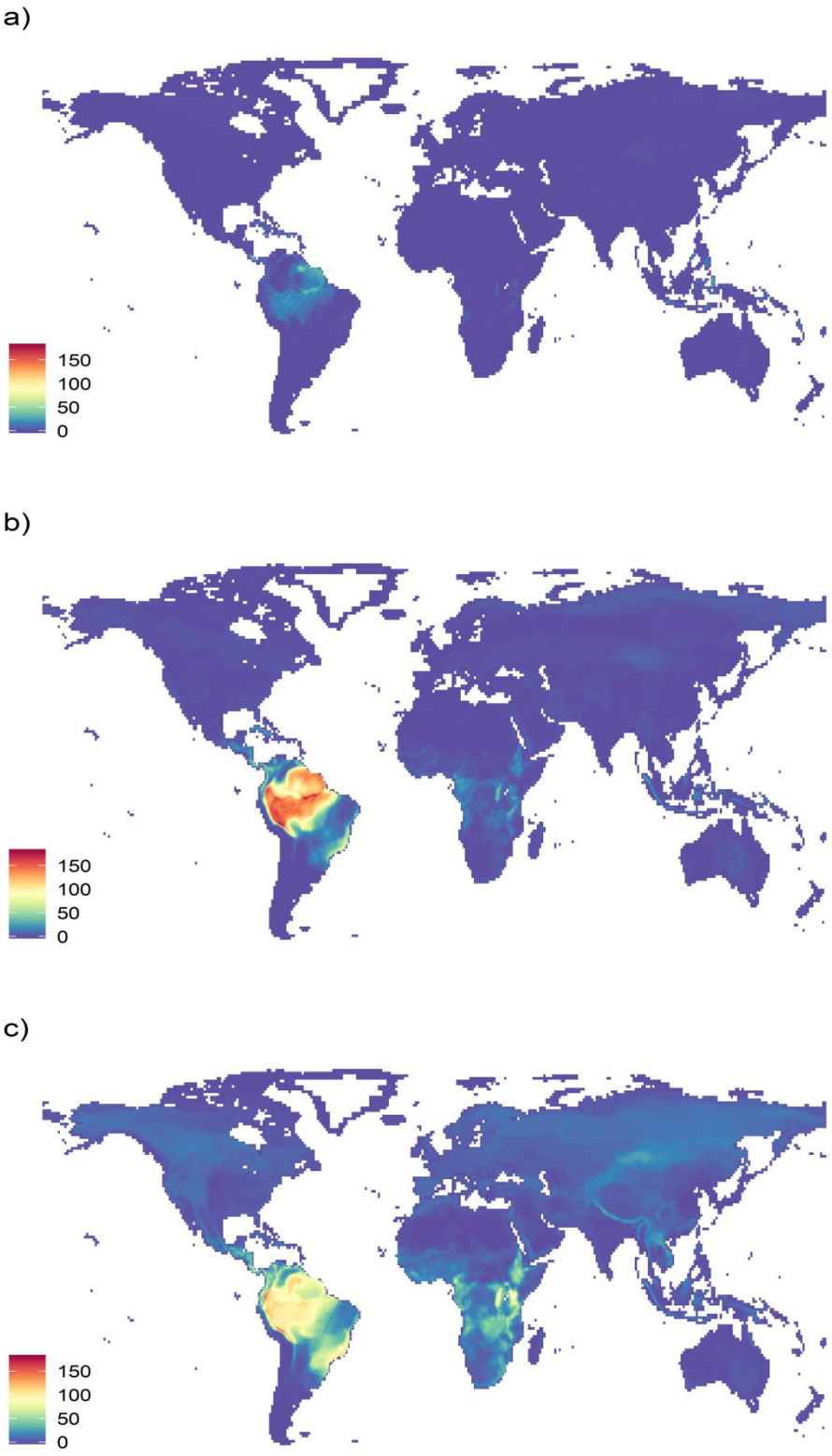


Figure 3.8: The current richness of species predicted to have the least overlap between their current and future range under a medium emission scenario (rcp45) by 2050. (a) species predicted to have no range overlap by 2050, (b) species predicted to have ≤ 25% overlap and (c) species that have < 50% and >25% overlap between their current and future range.

3.4.5 Range changes across different latitudes, altitudes and range sizes

Splitting the 9,196 species by latitude into bands based on their range centroids, highlighted significant differences in the projected impact of climate change on birds across different latitudes (Kruskal-Wallis, Proportional range change: $H=274.82$, $p < 0.01$; Range overlap: $H=255.08$, $p <0.0001$; Distance between range centres: $H=827.26,08$, $p <0.0001$). Significantly higher percentage range declines are projected for species at high northern latitudes (> 60°) and for species of tropical latitudes south of the equator (0° to -23°). By contrast, for species of high southern latitudes (-40° to -60°) increasing ranges are projected in future (Figure 3.9). Changes in the degree of range overlap for species of different latitudes between the present and future period are similar in patterns to the changes in range extent, with significantly lower range overlap for species of high northern latitudes (> 60°) and tropical latitudes south of the equator (0° to -23°) but higher range overlap at high southern latitudes (-40° to -60°) (Figure 3.10,). The distance between the current and future range centres of species are significantly greater at northern hemisphere temperate (60° to 40°) and high (> 60°) latitudes (Figure 3.11, Table S3.1 for post-hoc pairwise comparison).

Projected changes in ranges extents under climate change differed for narrow and wide range species. (Kruskal-Wallis, Proportional range change: $H=17.7$, $p < 0.0001$; Range overlap: $H=761.65$, $p < 0.0001$; Distance between range centres: $H=898.15$, $p < 0.0001$). Range restricted species (< 50 cells) are projected to experience the largest range declines, and very wide ranging species (> 2500 cells) have significantly less relative range declines than all other species (Figure 3.9). Narrow ranging species (<50 cells) have the lowest percentage range overlap between their current and future ranges, whereas wide ranging species (> 2500 cells) have the highest range overlap. Across all species, narrow ranging species have the smallest distances (km) between their current and projected future range centroids (Figure 3.11; Table S3.2 for post-hoc pairwise comparison).

Future climate change is likely to have differing degrees of impacts for species currently occurring at different altitudes (Kruskal-Wallis, Proportional range change: $H=178.28$, $p < 0.0001$, Range overlap: $H=119.08$, $p < 0.0001$, Distance between range centres: $H=18.59$, $p < 0.0001$). Species occurring at a minimum altitude of >1500 m have significantly higher range losses than species with lower minimum altitudes (Figure 3.9) and have significantly less range overlap between the current and future periods (Figure 3.11; Table S3.3 for post-hoc pairwise comparison).

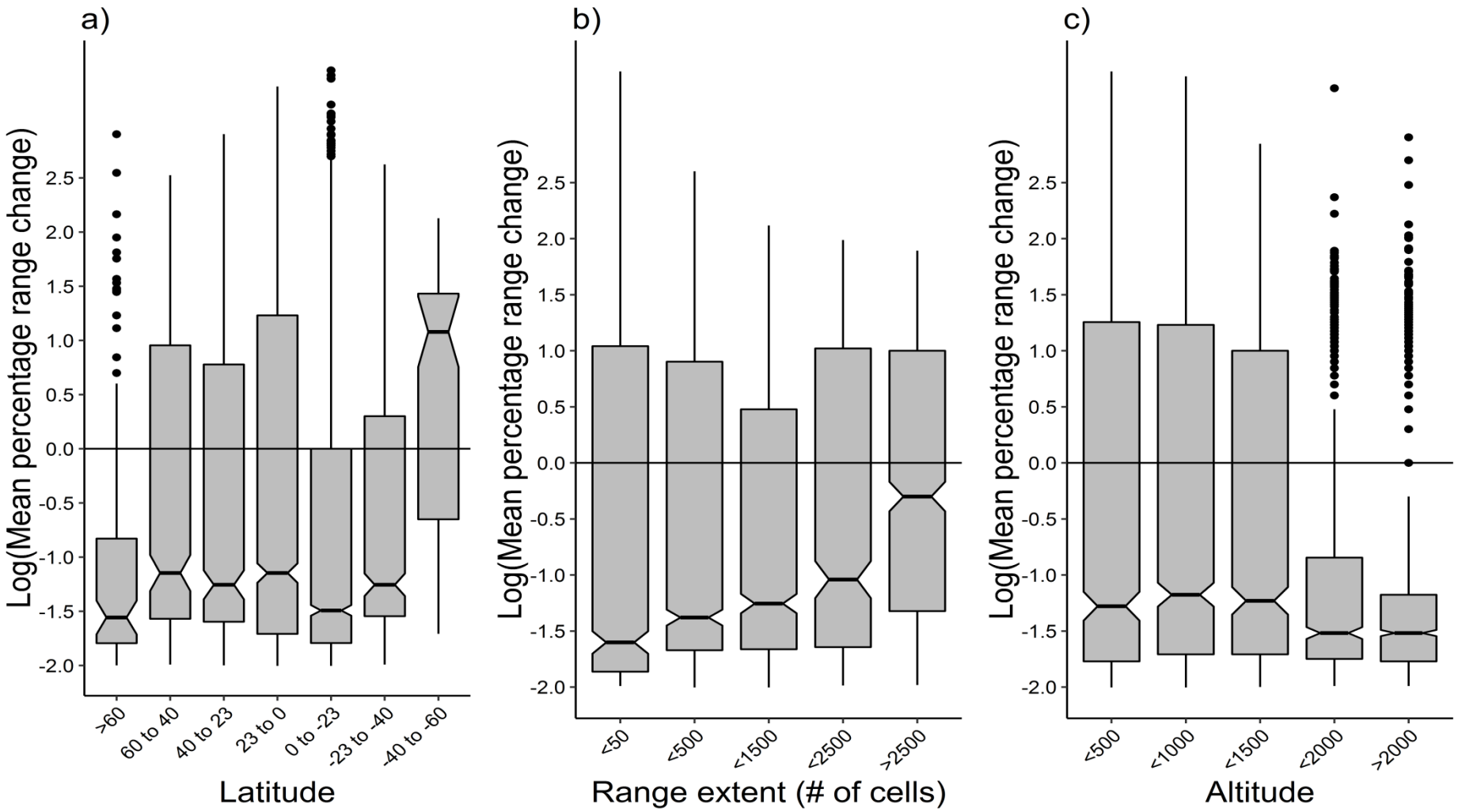


Figure 3.9: Mean percentage range change in relation to (a) latitudinal bands of species occurrence, (b) for species of differing current range extents, measured in the numbers of cells a species is present in (centre graph), and (c) for species with different minimum range altitudes.

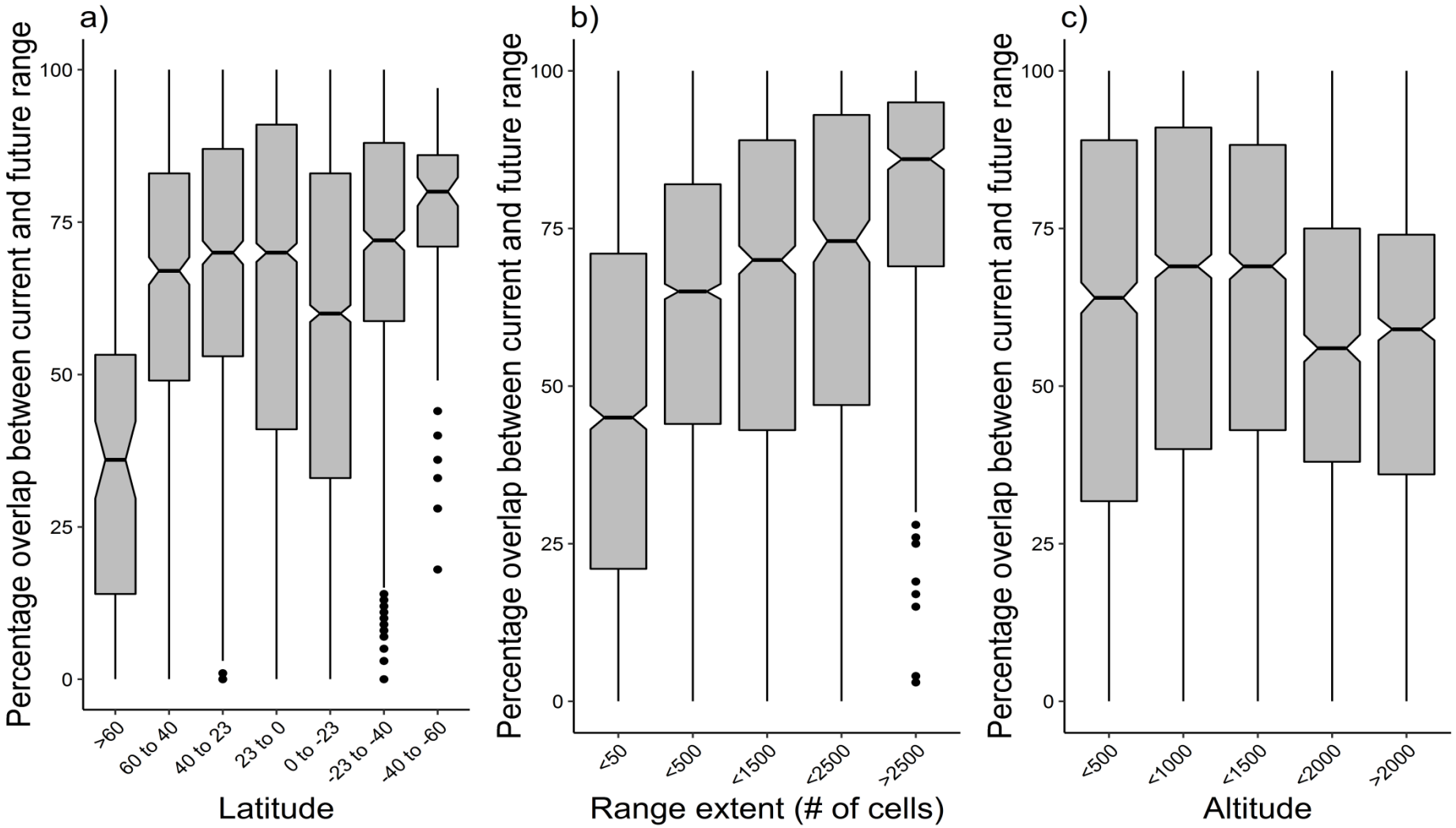


Figure 3.10: Mean percentage range overlap in relation to (a) latitudinal bands of species occurrence, (b) for species of differing current range extents, measured in the numbers of cells a species is present in (centre graph), and (c) for species with different minimum range altitudes.

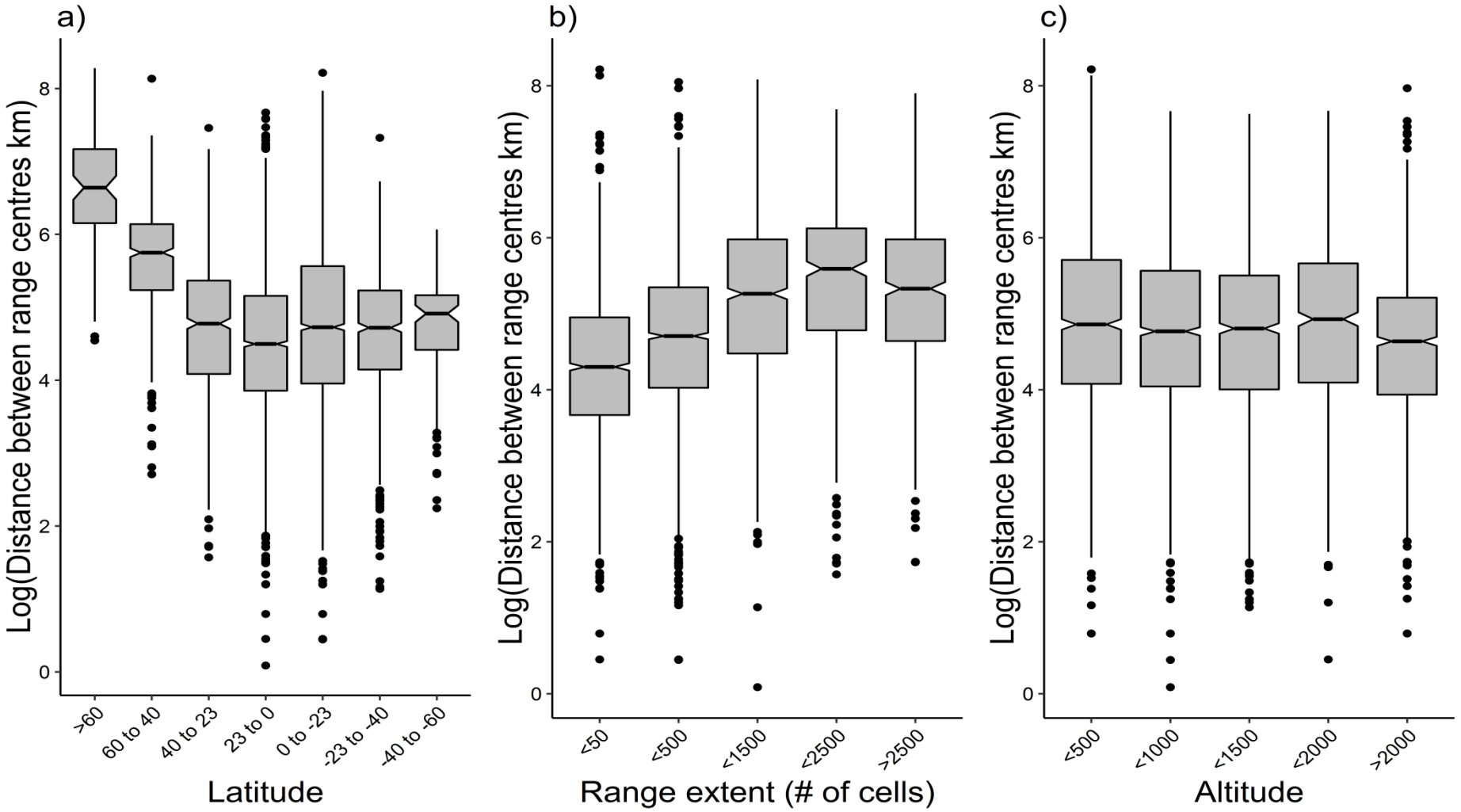


Figure 3.11: Mean distance (in km^2) between the current and future range centroid in relation to (a) latitudinal bands of species occurrence, (b) for species of differing current range extents, measured in the numbers of cells a species is present in (centre graph), and (c) for species with different minimum range altitudes.

3.4.6 Community changes

The dissimilarity between current and future avian communities within grid cells, based on the Bray-Curtis turnover, suggests highest turnover in the Amazon, the northern of the Palearctic and Nearctic, and in Southern Europe and the Middle East. Areas with comparably low turnover values include the Indian subcontinent, Australia, and the southern Neotropical region (e.g. Argentina and Chile). These turnover patterns match results of the species community analysis.

Across the Americas, the Nearctic was clustered into 12 avian communities (Figure 3.12). The projected future distribution of these communities is very similar to their current distribution, with small changes in the northern regions of the Nearctic. Some areas in the Northern Nearctic are projected to contain novel communities in future (Figure 3.12, (b)). The Panamanian realm was aggregated into 22 avian communities, with 15 located on the mainland and 7 on the Caribbean Islands (Figure.3.12, (c)). The future distribution of mainland communities is very similar to current patterns. By contrast, 5 of the 7 communities of the Caribbean Islands are projected to disappear in future (Figure 3.12, (d)). The Neotropics were clustered into 15 communities. Across the Neotropics, distinct changes in community distribution and composition are projected in future, with large areas of novel community types appearing in the Amazon region and several of the tropical rainforest communities declining in extent (Figure 3.12, (f)).

For Africa and the Middle East (Figure 3.13), predicted avian community changes are less severe than for the Neotropics. Afrotropical birds were grouped into 22 distinct communities. The predicted future distributions of the Afrotropical species communities largely remain unchanged, with only minor changes in the north of the Afrotropical realm and novel communities in the tropical shrubland areas in the south (Figure 3.13, (b)). Madagascar was grouped into five avian communities. The predicted future pattern of the species communities was similar for the inland communities, but the coastal communities are projected to disappear or to change into novel communities. There is small area assigned to a novel community-type in future in the south of the island (Figure 3.13, (d)). The Saharo-Arabian realm was clustered into 24 communities. The predicted future distribution of the communities of the Saharo-Arabian realm is similar to the current patterns, though with several areas of novel communities across the desert regions of North Africa and the Arabian Peninsula (Figure 3.13, (f)).

Looking at South East Asia and Australia, there were eight avian communities defined across the Oriental realm. These community distributions remained largely unchanged in future, besides areas of the Indonesian islands and the Philippines having novel communities and changes to the coastal communities along the Indonesian Islands (Figure 3.14, (b)). The Sino-Japanese realm was split into

12 distinct communities, with two communities in Japan and 10 communities on the main land (Figure 3.14 (c)). The future distribution of the communities looks very similar with only some changes along the coastal cells of Japan, as well as a cluster of cells in the subtropical humid forest in the eastern part of the realm (Figure 3.14 (d)). The Oceanian realm was split into 17 communities (Figure 3.14, (e)). These communities have a very similar distribution in 2050, besides some cells having novel communities along the South coast of Papua New Guinea and the Northern coastal community of Papua New Guinea being replaced by surrounding communities (Figure 3.14, (f)). The Australian realm is split into 18 communities, with two distinct communities each in New Zealand and Tasmania and 14 communities on mainland Australia. In future, the communities in the Australian realm are projected to remain largely unchanged though with substantial areas of novel communities in central Australia and in the North of New Zealand and Tasmania (Figure 3.14, (h)).

Looking at the Palearctic, the Western Palearctic is split into 16 communities, with 6 distinct communities across Canada and Greenland and 10 distinct communities for Europe. The future pattern of community changes, with southern communities extending northwards and novel communities that are appearing in the Mediterranean as well as some clusters of novel communities in Canada and Greenland (Figure 3.15. (b)). The Eastern Palearctic is divided into 19 distinct communities. The broad pattern of species communities remains under future prediction but a distinct band of novel communities appears across the northern Tundra as well as several clusters of novel communities in the South West of the Eastern Palearctic (Figure 3.15, (d)).

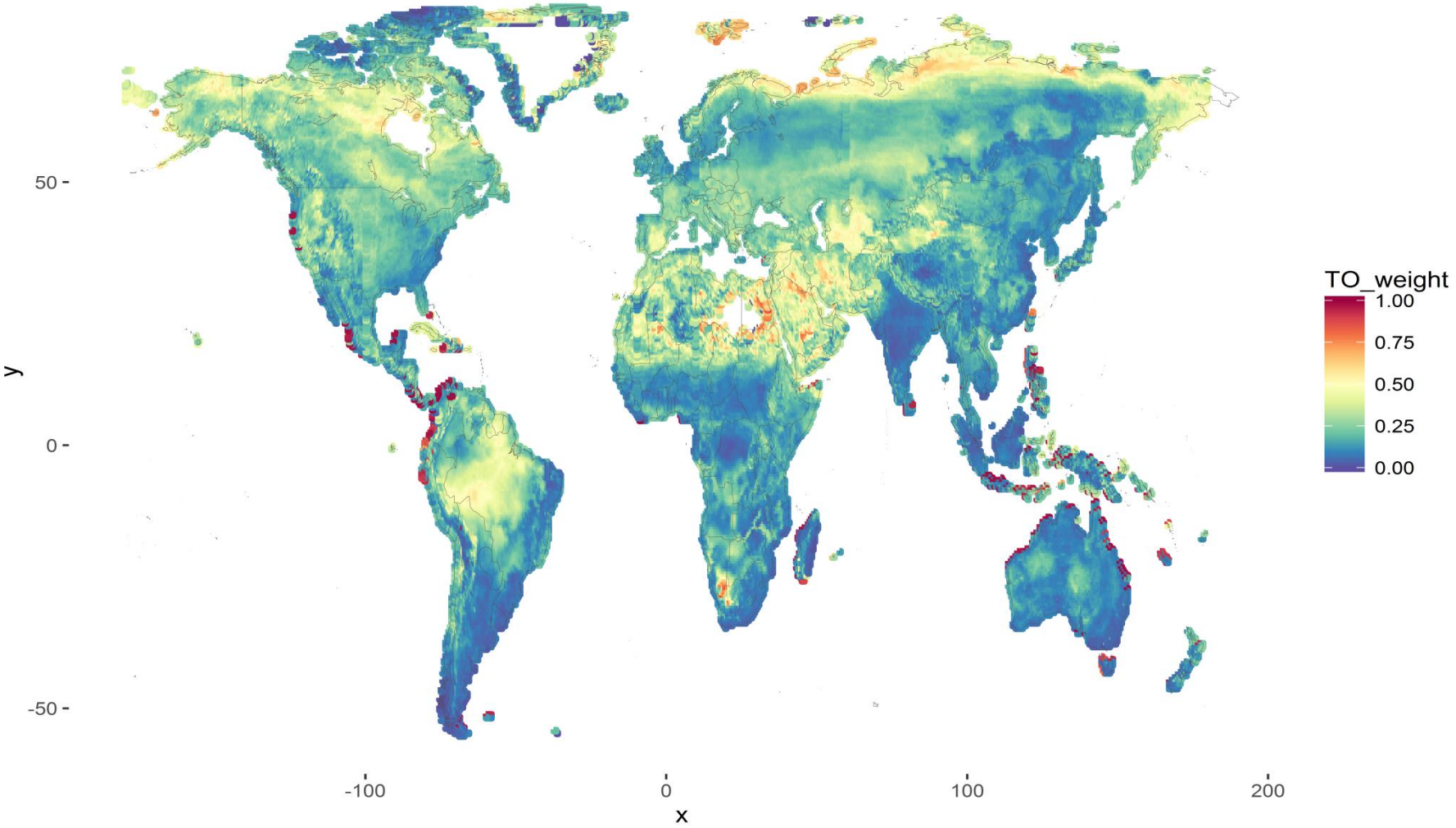


Figure 3.11 Bray-Curtis dissimilarity for each grid cell between the predicted current and future (2050) species community under a medium emission pathway (rcp45). All predictions are thresholded and based on the median ensemble result from the species distribution models. The future predictions are based on the mean predictions from the three used GCMs (CCSM4, GFDL-CM3, HadGEM-2ES) and a medium emission pathway (rcp45).

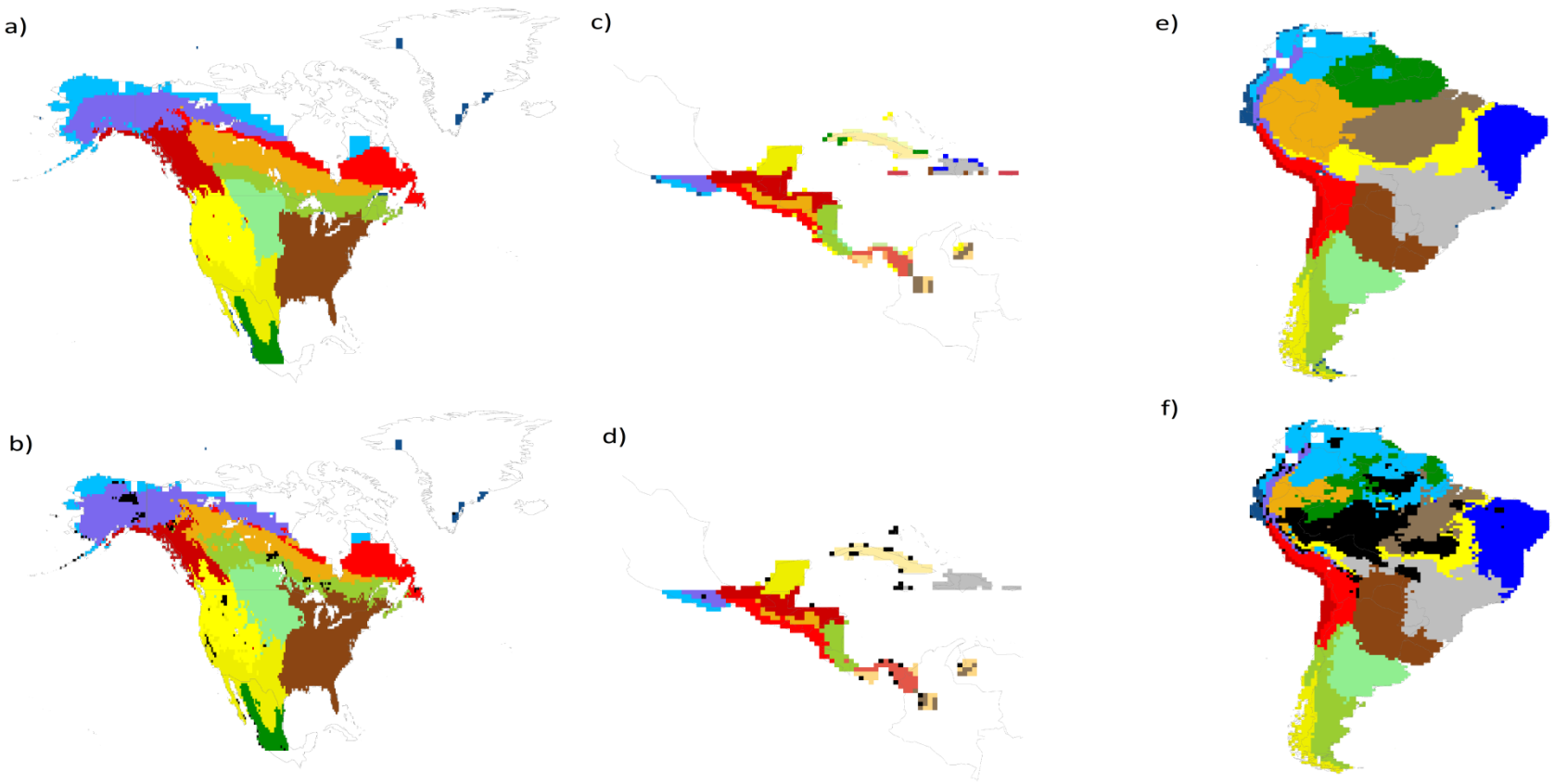


Figure 3.12: Changes in broad scale community classifications for the Americas. The top graphs represent the current community classifications (left to right, the Nearctic realm (12 communities), the Panamanian realm (22 communities) and the Neotropical realm (15 communities)). The bottom graphs represent the future community classifications based on the mean predictions across the three used GCMs (CCSM4, GFDL-CM3, HadGEM-2ES) and a medium emission pathway (rcp45). All predictions are thresholded and are based on the ensemble median results from the species distribution models. The current community classifications are based on the hierarchical cluster analysis for each realm. Future community classifications are based on the classification of the most similar current grid cell. Cells coloured in black in the bottom graph represent novel communities with no analogue current community.

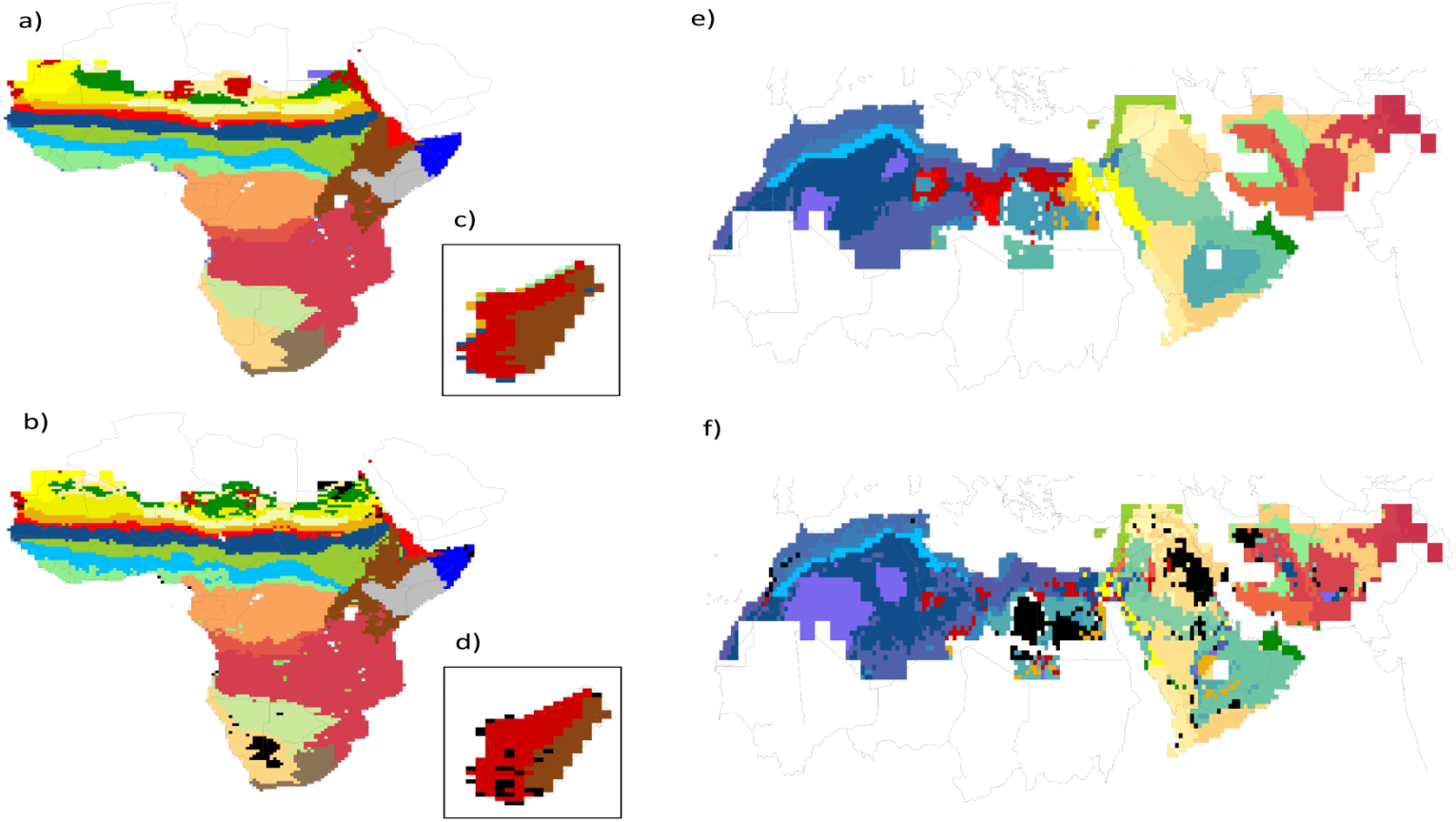


Figure 3.13: Changes in broad scale community classifications for the Africa and the Middle East. The top graphs represent the current community classifications (left to right, the Afrotropical realm (22 communities), the Madagascan realm (5 communities) and the Saharo-Arabian realm (24 communities)). The bottom graphs represent the future community classifications based on the mean predictions across the three used GCMs (CCSM4, GFDL-CM3, HadGEM-2ES) and a medium emission pathway (rcp45). All predictions are thresholded and are based on the ensemble median results from the species distribution models. The current community classifications are based on the hierarchical cluster analysis for each realm. Future community classifications are based on the classification of the most similar current grid cell. Cells coloured in black in the bottom graph represent novel communities with no analogue current community.

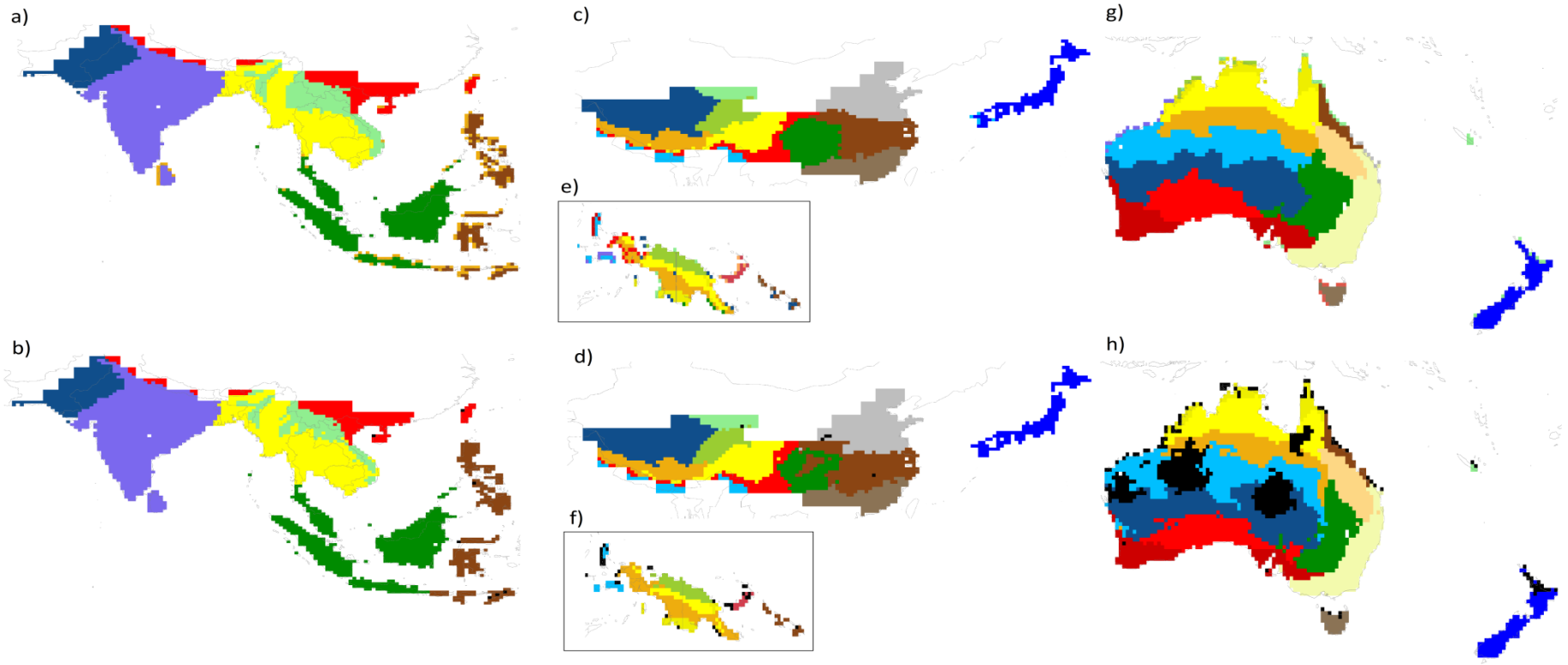


Figure 3.14: Changes in broad scale community classifications for the South East Asia and the Australia. The top graphs represent the current community classifications (left to right, the Oriental realm (8 communities), the Oceanic realm (17 communities), the Sino-Japanese realm (12 communities) and the Australian realm (18 communities)). The bottom graphs represent the future community classifications based on the mean predictions across the three used GCMs (CCSM4, GFDL-CM3, HadGEM-2ES) and a medium emission pathway (rcp45). All predictions are thresholded and are based on the ensemble median results from the species distribution models. The current community classifications are based on the hierarchical cluster analysis for each realm. Future community classifications are based on the classification of the most similar current grid cell. Cells coloured in black in the bottom graph represent novel communities with no analogue current community.

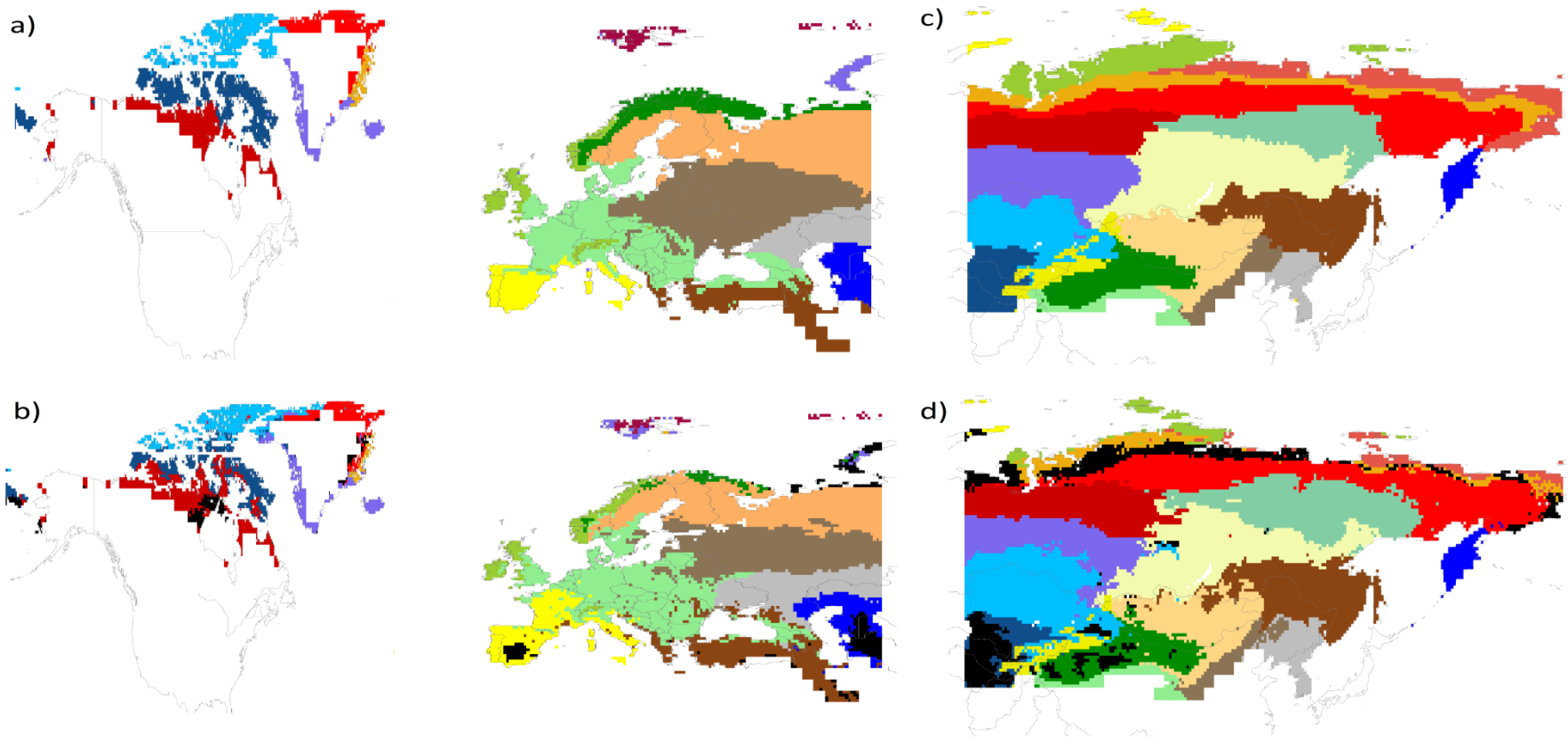


Figure 3.15: Changes in broad scale community classifications for the Palearctic. The top graphs represent the current community classifications (left to right, the Western Palearctic realm (16 communities) and the Eastern Palearctic (19 communities)). The bottom graphs represent the future community classifications based on the mean predictions across the three used GCMs (CCSM4, GFDL-CM3, HadGEM-2ES) and a medium emission pathway (rcp45). All predictions are thresholded and are based on the ensemble median results from the species distribution models. The current community classifications are based on the hierarchical cluster analysis for each realm. Future community classifications are based on the classification of the most similar current grid cell. Cells coloured in black in the bottom graph represent novel communities with no analogue current community.

3.5 Discussion

3.5.1 Changes in global species richness patterns

Global species richness patterns are projected to change markedly by 2050 under the medium emission scenario (rcp45) presented here (Figure 3.4). The most noticeable changes occur in the species rich tropical regions; with high losses in the Amazon basin and East Africa and some of the islands in South-east Asia but also the northern Palearctic has a high proportion of species with decreasing ranges (number of species Figure 3.4 and proportion of species Figure S3.7). These areas with projected highest impact of climate change on species ranges overlap with the areas highlighted by Williams et al. (2007) as being at high risk for disappearing and novel climates. They predict the Andes and eastern Africa to be particularly at risk from disappearing climates and the Amazon amongst other areas to be at especially high risk to have novel climates in future. Large range loss projections based on climate change alone for the tropics is concerning, since habitat loss is already a major driver of range reduction and extinction for tropical birds (Dirzo & Raven, 2003; Sodhi *et al.*, 2011). Recent land use change has been especially high in the tropics, with one third of Brazil having already been transformed (Ferreira *et al.*, 2012). The situation is similarly severe in South-east Asia, with Indonesia having overtaken Brazil, as the regions with the highest current deforestation rate globally (Margono *et al.*, 2014). This highlights the urgency of conservation actions needed in these areas.

Comparing the projected changes in species richness in the future from models that use unlimited versus realistic dispersal assumptions, indicates that richness declines are predicted to be much more severe under realistic dispersal assumptions. This emphasises the importance of considering realistic dispersal ability of species, as has also been demonstrated in regional European studies (Araújo *et al.*, 2006; Thuiller *et al.*, 2006). The summed natal dispersal ability of species across a time period (controlling for generation length) is not an ideal metric in some scenarios, such as those that demand a single long-distance movement to cross a barrier (such as occurs in relation to some islands, and hence our modification of the dispersal assumptions in these situations). However, in most cases we assume that the resultant projections will be more realistic than using unlimited dispersal. This has been shown in other studies simulating historical range shifts in species (Willis *et al.*, 2009c), and in unpublished work (by S.Willis) simulating avian colonists to the UK in recent decades. To further improve the predictions, dispersal ability could have been accounted for on an annual basis, using a raster of the landmass and only allowing a species to move on from suitable cells in the year before, but this was too computationally intense to be incorporated for all species of the world. Moreover, this would require good data on maximum individual dispersal events for species, which is lacking for most species of the world.

3.5.2 Changes in range extent and overlap

Changes in range extent and overlap were projected for the vast majority of terrestrial birds, with 7,648 of the species modelled being predicted to experience range changes >10% of their current range by 2050. About one-fifth of the modelled species projected to experience major range losses (>75% decline in range extent projected) or to have no climatically suitable areas remaining in future. Similarly, 2,059 species have <25% overlap between their current and future range, with 951 species having no overlap between current and future climatically suitable regions. Hence, the projected impact of climate change on species ranges is severe. The distribution of the species projected to lose range and range overlap reflects the global pattern of changing species richness projected in future. The majority of species projected to experience highest range losses (Figure 3.7) and have least range overlap (Figure 3.8) are located in the tropics, mainly the Amazon basin and Eastern Africa, but the Palearctic also has large number of species with shrinking ranges predicted for the future. The projected areas with high numbers of species with significant range losses cannot be explained as an artefact of cells with high species richness also having high numbers of species with declining ranges and reduced overlap; proportional plots of species with declining range and reduce range overlap in cells highlight very similar areas as those for total species numbers. These patterns agree with earlier studies that indicate tropical montane species to be especially vulnerable to climate change (Williams *et al.*, 2003; Şekercioğlu *et al.*, 2012) as well the already observed trend of declines and northwards movement in northern boreal species (Virkkala *et al.*, 2008; Laaksonen & Lehikoinen, 2013; Virkkala & Lehikoinen, 2014). Furthermore the high proportion of species predicted to lose range and range overlap in the northern Palearctic could also reflect that northern species tend to be more sensitive to climate whereas southern species are more sensitive to land use change (Howard *et al.*, 2015).

3.5.3 Range changes across different latitudes, altitudes and range sizes

Splitting species based on the latitude, range extent and altitude of their range indicated that range losses were significantly higher for species occurring at high latitudes (>60°) and for those of the southern equatorial zone (0° to -23°). In both of these areas species also have significantly lower range overlap compared to the other areas. Shifts in range were greatest at high latitudes but, unlike range extent changes and overlap figures, range shift in the southern equatorial zone was no different from that for species from other areas. The tropics harbour high numbers of birds, with poor dispersal ability (Şekercioğlu *et al.*, 2002) and often comparably small range size (Rapoport, 1975; Stevens, 1989); thus, these species might respond to climate change with reduced range size and overlap due to the inability to track suitable climate space rather than losing range overlap due to large range shifts.

Avian species with small range size have been consistently associated with higher extinction risk (Harris & Pimm, 2008; Lee & Jetz, 2011). Additionally, small range species have been found to often occur in areas with rare climate, which also puts them at high risk from climate change (Ohlemüller *et al.*, 2008). Splitting the species based on range size, supports the assumption that species with restricted ranges could be more vulnerable to climate change, with significantly higher range losses in the group of species with restricted climate (< 50 cell occupied) compared to other groups and significantly less range loss for wide ranging species (>2500 cells) compared to the other groups. Restricted range species (< 50 cell) have the lowest projected range overlap, whereas wide ranging species experienced the highest range overlap (>2500 cells) between the two periods. Range shifts were lowest for restricted range species (< 50 cell), which could again reflect that species with very narrow distributions tend to have lower dispersal abilities.

Species occurring at high altitudes (min altitude >1500 metres) are projected to have significantly higher greater range loss and lower range overlap between their current and future distribution, than are species of lower altitude distributions. This agrees with earlier studies showing that species in rare climates, which are often located at high elevations and in areas with strong altitudinal gradients (Ohlemüller *et al.*, 2008), are predicted to be highly vulnerable to climate change. Nevertheless species of lower elevations have been found to be more likely to be classified to be at contemporary extinction risk (White & Bennet, 2015). This is probably due to the fact that the IUCN threat categories do not directly account for risk from climate change (White & Bennett, 2015) and because, to date, habitat loss and degradation, which are more prevalent at lower elevations, have been the major threats to species. The predicted range changes for species at high altitudes indicate that, in future, there might well be a stronger correlation between species occurring at high elevation and extinction risk.

3.5.4 Community changes

The changes in species turnover simulated for cells between the present and 2050, match well with the projected patterns in range changes. Turnover in community composition is especially high in the Amazon basin, the Mediterranean and the northern Palearctic, but Eastern Africa and parts of South East Asian also have comparatively high values. It can also be seen that species-poor areas such as the Saharan desert often have very high turnover. It needs to be considered that turnover is relative to the current composition of a cell, thus for cells with a very low richness, high turnover values are more likely to occur (e.g. if there is a cell containing one species and another species moves in this will result in a much higher turnover value than a species moving new into a cell that already has 300 species). Overall, the predicted turnover values make biological sense. Southern Europe has higher projected turnover than northern Europe, which is consistent with earlier studies

forecasting especially northern African species to colonize the South of Europe (Barbet-Massin *et al.*, 2010, 2012a). Across Scandinavia and the Palearctic an opposite pattern can be observed, with higher turnover in the northern areas than in the South, this is consistent with studies observing a northward trend in boreal bird species, as well as slower range shifts along the southern range boundaries of these species (Virkkala & Lehikoinen, 2014).

The distribution of the current communities largely makes ecological sense. Looking at the Americas, the communities in the Nearctic which largely mirrored the broad scale ecoregions of North America (EPA, 2016), with areas such as eastern temperate forests, northern forests, the great plains, showing very distinct species communities (Figure 3.12, (a)).The Neotropics similarly mirror the broad ecoregions of the area (Olson *et al.*, 2001), with separate avian communities identified for the tropical rainforests, and tropical moist forests and the tropical Andean mountains (Figure 3.13, (e)).

For Africa and the Middle East, distinct communities were identified for the subtropical mountainous areas in the south-east, the tropical shrubland and tropical dry forest in the south, the tropical rainforest in Central and West Africa and several latitudinal bands of communities from the Sahara changing to the tropical rainforests (Olson *et al.*, 2001), (Figure 3.13, (a)). Madagascar is divided into five communities, one comprising the sub humid and lowland forest species in the centre and east of the island, one comprising the dry deciduous forests and the arid areas in the west and south (Brown *et al.*, 2016), and three coastal/mangrove communities (Figure 3.13, (c)). The Saharo- Arabian realm harbours 24 communities, of which 18 smaller communities are located in North Africa and the Arabian Peninsula and an additional five communities were defined in Central Asia. The Mediterranean forest, wood and shrublands north of the Sahara (Olson *et al.*, 2001) form another distinct community (Figure 3.13, (e)). This realm matches less well with the underlying ecoregions.

Looking at the realms across South East Asia and Australia, the observed communities match again more closely with the larger Ecoregions. The communities on the Australian mainland broadly match the Australian ecoregions, with a community defined each for the mediterranean woodlands in the South, the temperate broadleaf forests in the south east, the temperate grasslands in the East, and the tropical rainforest along the north-east coast. The Central desert and shrubland is divided in three distinct bands, and so are the tropical and subtropical grassland in the North of the continent (Australian Government, 2013) (Figure 3.14, (g)). The Oriental realm is split in six communities in South East Asia and two communities on the Indian subcontinent following the arid and tropical areas (Figure 3.14, (a)).

Across the Palearctic, the European communities largely match previously described ecoregions, having a distinct species community each for the Mediterranean area in the South, the boreal area in the North East and the Northern alpine area of Scandinavia (EEA, 2017), as well as 7 distinct communities across central Europe and the UK (Figure 3.15,(a)). The eastern Palearctic is split into 5 different species communities for the boreal forests stretching across the Palearctic and 4 distinct bands of communities across the northern Tundra areas (Figure 3.15, (c)).

Areas predicted to experience changes in avian communities broadly correlate with regions of high turnover and with large numbers of species predicted to decline in range extent and/or experience range shifts. Novel communities are projected especially in the Amazon basin, the Mediterranean and the Northern Palearctic. Novel communities are also predicted in some areas with very low richness, such as the Saharan desert, the Arabian peninsula and central Australia. For these low richness areas, relatively minor change in species composition, in cells with very low species numbers, could alter a community allocation. The changes in community composition are in line with a wide array of studies that investigated individual responses to climate change and suggested that these individual responses could have pronounced impact on future community compositions (Bakkenes *et al.*, 2002; Peterson *et al.*, 2002; Thuiller *et al.*, 2005b) and predicted the formation of novel non analogue communities (Huntley, 1991; Walther, 2003; Stralberg *et al.*, 2009). The reshuffling of species communities and especially the formation of novel non-analogue communities can have profound consequences for biodiversity and ecosystem functioning (Chapin III *et al.*, 2000; Walther, 2010). Species in areas with changing community composition or novel communities will face new pressures, such as changes in competition or predation (Strauss *et al.*, 2006; Blois *et al.*, 2013; Alexander *et al.*, 2015), and may deliver very different ecosystem services in future, possibly to the detriment of the local human populations as well as to biodiversity. Highlighting areas were novel communities will arise is important, since these will be especially challenging areas for conservation planning (Stralberg *et al.*, 2009).

For the community composition analysis in this chapter I used a k-means cluster analysis to pre-determine the number of communities to assign in each zoogeographic area. I chose the number of clusters that explained 95% of the remaining variation due to computational and time limitations I restricted the pre-selection of the number of clusters to just a single method. Ideally, to make the number and definition of clusters more robust, multiple metrics to validate the chosen number of clusters should be used. Different possibilities to assess the strength of the cluster solution could be using the Xie-Beni Index (Xie & Beni, 1991) or using the pair-wise correlation between cluster solutions to assess the cluster stability (Mahlstein & Knutti, 2010).

3.5.5 The presented projections

Throughout this chapter I have presented results for only a medium emission scenario (rcp45) and for the period up to 2050; this represents a global mean surface temperature change of 1.4°C (0.9°C -2°C) (Stocker *et al.*, 2013). This rcp pathway might not best represent climatic change to 2050. Thus, it would be helpful to compare the rcp 45 projections with the two other pathways (rcp26 and rcp85) for which SDM models were produced, to see how the observed impacts differed. However, to do this robustly would have considerably extended this chapter, and hence the decision was made to focus on only a medium emission scenario. Whilst richness and range loss data based on these two other scenarios are included as supplementary material, the time necessary to produce community projections for these alternate scenarios precluded their inclusion in the thesis. Producing these alternate community projections, for longer time periods and alternate scenarios, is an area of future research that I intend to pursue. The comparison of the projected range changes based on the three different GCMs shows that predictions for individual species vary between the different GCMs, but the overall predicted patterns are similar. The projected species distributions are based on ensemble median predictions across the SDMs. Although it has been shown that there is high variability between the predictions of different SDMs (Bagchi *et al.*, 2013), using ensemble modelling improves the predictions. Even though the future predictions for some individual species might not be highly accurate, which is unavoidable when modelling ~9000 species the overall pattern might not be altered by this.

3.5.6 Other impacts on species ranges aside from climate

For this chapter, the SDMs were based solely on climate suitability, thus the presented results might underestimate or over-estimate the range alterations species will experience. Land use change is an important driver of species range changes and will make the projected range losses more severe. Especially in the tropics, land use changes are projected to have a major impact on species ranges and extinction risk (Jetz *et al.*, 2007). For example, Indonesia does not stand out in the analyses in this chapter as having high projected losses compared to other tropical areas, but having the highest deforestation rate in the world (Margono *et al.*, 2014) this pattern might well be very different had the models included both current and projected future land use change, in both facilitating movement and in restricted the availability of suitable areas to include only those that have both suitable climate and habitat. This could be a very important area for future research. Additionally, the SDMs ignore factors such as competition, inter-specific relationships (Araújo & Luoto, 2007; Franklin, 2009) or genetic adaptation (Thomas *et al.*, 2001; Harte John *et al.*, 2004; Thuiller *et al.*, 2008). All of these factors could impacts on species range changes, and are likely to change the observed pattern. These limitations to SDMs have been recognized (Pearson & Dawson, 2003) and

recently developed modelling approaches are starting to incorporate these factors (Pollock *et al.*, 2014; Zurell *et al.*, 2016). However, for a study on a global scale that includes almost all terrestrial birds, incorporating such factors it is not yet possible, largely as a result of a lack of documentation of such factors for species.

3.5.7 Implications for conservation

The results I present in this chapter give an overview on how terrestrial species richness patterns are affected by climate change. I highlight areas that harbour high numbers of species whose ranges are projected to be affected by climate change. Pinpointing these areas can support conservation planning (Hannah, 2008). Additionally, I simulate that species with restricted ranges, at high altitudes, as well as high latitudes will experience greater range loss compared to other species. This too is valuable information for the conservation of species. Finally I provide a first overview on were species communities might be prone to be reshuffled most and were novel communities might arise based on climate change. Due to the high unpredictability of changed and novel communities and the challenge they will provide for conservation (Stralberg *et al.*, 2009) it is important to be able to pinpoint were these changes are prone to happen.

Chapter 4

Effects of future climate change on the coverage provided by the Important Bird and Biodiversity Area network for the world's terrestrial birds

4.1 Abstract

Two of the principal responses of species to recent climate change have been changes in range and abundance; and a global reshuffling of the geographic distribution of species is currently occurring. Such range changes may cause species to move out of the protected areas (PAs) in which they currently occur and, consequently, affect the ability of PA networks to protect species. Depending on the changes in species protected within an individual PA, it my decrease or increase in its future conservation value. Identifying PAs that will provide suitable conditions for species under future climate change and those that will lose suitability can support conservation planning.

Here, I explore the potential impact of projected range changes on the ability of BirdLife International's Important Bird and Biodiversity Area (IBA) network to protect the worlds' terrestrial birds. The IBA network is an idealized network of more than 12,000 areas that are of importance for the conservation of the world's birds. I use species distribution models (SDMs) to produce dispersal-linked projections of range changes for the majority (9,196 species) of the world's terrestrial birds. I calculate future (2050) community turnover for each IBA and assign the IBAs to climate change adaptation strategies based on the projected emigrants and colonists to a site. Additionally, I identify potential shortcomings in the future coverage of the IBA network for terrestrial birds, using a gap analysis. I intersect simulated future distributions for all birds with the global IBA network and identify species whose representation in the network is projected to change markedly. I find that terrestrial bird species currently have a high coverage by the IBA network with only 267 'GAP species' but that an additional 311 species will move of the IBA network by 2050. Overall 4,319 species are projected to have reduced IBA cover by 2050. Species turnover in IBAs is markedly high in the Amazon, the northern Palearctic and southern Europe, especially Spain. IBAs with comparatively low species turnover are located in west and central Africa, including Chad, Sudan and the Central African Republic, as well as across the Indian sub-continent and eastern China. Although the number of species projected to lose all IBA coverage is relatively low, the number of species projected to have reduced IBA coverage by 2050 is high. This, combined with the high turnover values that we project for some IBAs, highlights the major impact future range changes are projected to have on the IBA network. The findings support the urgent need to consider future projections in the management of protected area networks.

4.2 Introduction

The Aichi biodiversity targets are set by the Convention of Biological Diversity (CBD), to achieve a reduction in biodiversity loss by 2020 (CBD, 2010). One of the aims of these targets is to prevent the extinction of threatened species and to improve their conservation status by 2020 (Target 12). Another aim of the Aichi targets is to expand the global protected area network to conserve at least 17% of the global landmass of terrestrial area and inland water, and a further 10% of coastal and marine ecosystems (Target 11) (Convention on Biological diversity, 1992). Protected areas (PAs), set aside to safeguard biodiversity, are a cornerstone of species conservation (Hambler, 2004). The number of protected areas has grown substantially over recent decades, yet the protected area network remains far from complete, in terms of protecting species diversity (Brooks *et al.*, 2004; Rodrigues *et al.*, 2004b; Rodrigues *et al.*, 2004a). To reach CBD Target 11, 5.8 million km^2 of additional PAs are required by 2020. These additional PAs provide an opportunity to strategically fill gaps in the current PA coverage (Hannah, 2008; Venter *et al.*, 2014). However, the achievement of these protection goals in the longer term is complicated by climate change, which is projected to impact the protected area network in various ways. One obvious impact of climate change is that species may track suitable climate and, consequently, move out of PAs, in some cases changing the fundamental ecology of a PA (Worboys *et al.*, 2006; Hannah, 2008). That species are changing their ranges under climate change is widely accepted (Parmesan *et al.*, 1999; Walther *et al.*, 2002; Parmesan & Yohe, 2003; Thomas *et al.*, 2004; Chen *et al.*, 2011) and changes in species ranges have been predicted to reduce species coverage by protected areas (Araújo *et al.*, 2004; Coetzee *et al.*, 2009; Araújo *et al.*, 2011). Furthermore, species range changes could lead to novel communities within protected areas, due to species moving in and out of the boundaries of protected areas (Hannah *et al.*, 2007). As a consequence, high community turnover has been predicted for some PAs (Hole *et al.*, 2009; Bagchi *et al.*, 2013).

Protected areas are almost always static in their distribution, and networks of sites are based on the current (or sometime historical) distribution of biodiversity (Worboys *et al.*, 2006). This characteristic could cause the protected area network to become less effective in safeguarding global biodiversity, as species alter their ranges under climate change (Willis *et al.*, 2009a). Studies estimating the future protective capability of the current protected area network have come to differing conclusions dependent upon the study area and extent (Araújo *et al.*, 2004; Kharouba & Kerr, 2010; Araújo *et al.*, 2011; Thomas *et al.*, 2012; Gillingham *et al.*, 2015). A network of European protected areas has been predicted to become less effective over time and to be no better at protecting priority species in future than a network of protected areas placed at random (Araújo *et al.*, 2011). By contrast, other networks in the UK as well as across Canada have been projected to retain some of the value they

currently provide into the future, or even increase in parts, in their importance for species conservation due to an increase in colonizing species (Araújo *et al.*, 2011; Thomas *et al.*, 2012; Gillingham *et al.*, 2015). Species distribution models (SDMs) have frequently been used to estimate the impacts of climate change on the future performance of protected area networks (Araújo *et al.*, 2004; Hannah, 2008; Willis *et al.*, 2009a). They can be used to simulate the current and future ranges of species, and consequently also the potential for gains and losses in PAs (Hannah, 2008).

To assess the coverage that a PA network provides to biodiversity, GAP analysis is a commonly used tool (Scott *et al.*, 1987; Burley, 1988; Jennings, 2000). A GAP analysis is a planning approach based on assessment of the comprehensiveness of existing PA networks and the identification of "gaps" in their coverage (Jennings, 2000). It was developed into a formal method by the USGS *Gap Analysis Program* using several spatially explicit datasets: a) species distributions, b) dominant vegetation cover types and c) conservation areas (U.S. Geological Survey, 2012b). GAP analysis can be used in conservation planning to evaluate the coverage provided to overall biodiversity or to individual taxa, as well as to optimize PA networks by identifying priority areas to improve the coverage provided by the network (Brooks *et al.*, 2004; Rodrigues *et al.*, 2004a). It has been used to evaluate the coverage of PA networks ranging in extent from global analyses to evaluation the performance of networks on a national scale (Powell *et al.*, 2000; Rodrigues *et al.*, 2004a; Abellán & Sánchez-Fernández, 2015).
Here I explore to what extent a global network of sites, designated to conserve the world's birds, will continue to provide protection for terrestrial birds in future and how the level of protections differs from current coverage. I am using the Important Bird and Biodiversity Areas (IBAs) of BirdLife International. Since the 1970s, BirdLife has been working on documenting and protecting all the places on Earth of greatest significance for the world's birds. It is an idealized network, highlighting areas important to conserve the world's birds and constitutes more than 12,000 areas. 28% of IBAs are fully protected but 49% lack any form of protection (Butchart *et al.*, 2012; BirdLife International & NatureServe, 2017). The strategic distribution of the IBAs, aiming to cover the minimum essential area to ensure the survival of a large number of species, makes them a cost effective and efficient tool for the conservation of the worlds' birds (BirdLife International & NatureServe, 2017). Since the protection of the IBA network is still being extended, information on the future performance of the individual areas within the network could give guidance to where efforts to increase the protection should be focused on. This could be done by highlighting those areas that remain important or even increase in their importance for the conservation of the worlds' terrestrial birds under future climate change.

I use species distribution models (SDMs) to project future ranges of the world's terrestrial bird species. I use these future range projections to estimate the turnover of terrestrial bird species within each IBA. Following this, I assign all terrestrial IBAs to the broad climate change adaptation categories, as developed by Hole et al. (2011), reflecting the degree of projected immigration and emigration of species. Each IBA is classified as being either: projected to increase in value, have high persistence of the current assemblage, or becoming more specialized under changing climate. There are five different climate change adaptation categories: 'High persistence', 'Increasing specialization', 'High turnover', 'Increasing value' and 'Increasing diversification'. To each of these categories different management actions and an overall management goal are assigned. The management actions are split into different categories, including actions regarding habitat restauration, translocation of species, disturbance regime management, potential increase of site extent or management of the landscape permeability (Hole *et al*., 2011). Additionally to assigning the IBAs to these different management categories, I undertake a species focused approach using a gap analysis to identify species simulated to be under-represented within the IBA network, both now and in the future.

The aim of this chapter is to assess the impact of climatically-induced range changes on the conservation of the world's terrestrial birds, to identify potential shortcomings of IBA coverage in future and to highlight potentially changing management needs of IBAs in future.

4.3 Methods

Species distribution data

I obtained global breeding range polygons from BirdLife International for 9196 bird species (BirdLife International & NatureServe, 2012). The distribution data was gridded as described in Chapter 3, using a 0.5° degree grid (55 x 55 km at the equator), with a minimum overlap of 10% for species that intersected with > 50 cell, and a 0.25° degree grid without the application of a minimum range overlap for species that intersected with < 50 cells. Pseudo-absences were selected using a distance weighted approach, as described in Chapter 2.

Climate data

The current bioclimatic data was obtained from WorldClim. I used the four bioclimatic variables selected in Chapter 2, temperature seasonality, maximum temperature of the warmest period, annual precipitation and precipitation seasonality. I predicted the future potential distribution of species for the time period centred around 2050 (average for 2041 – 2060), using three different global climate models (GCMs) CCSM4, GFDL-CM3 and HadGEM2-ES, as described in Chapter 3. The analysis and results in this chapter are based on a medium emission pathway (rcp45).

Species distribution models

I used three different approaches, to model the relationship between current species distributions and the four different bioclimatic variables, Generalized Linear Models (GLM), General Additive Models (GAM), and Random Forest Models (RF), as described in Chapter 3. I dealt with spatial dependence by splitting the data into 10 blocks following the world's Ecoregions, and subsequently building models based on 9 blocks and predicting to the left out block to assess performance, as described in Chapter 2, but using a 30:70 split for restricted range species as described in Chapter3.

Predictions

Species distributions were predicted to a species' realm of occurrence as well as the nearest neighbouring realms a species could move into (Chapter 3, Figure 3.1), for all species modelled on a 0.5° degree grid. Species on a 0.25° degree grid were predicted within a 1000 km radius of their current prediction, following the methods as described in Chapter 3.

Natal dispersal

Projected range changes, to the middle of the current century (2050), were restricted based on the natal dispersal ability of a species, following the methods described in Chapter 3.

Important Bird and Biodiversity Area (IBA) data

I obtained polygons for the global IBAs from BirdLife International. Due to the terrestrial focus of the study I only included IBA polygons that are overlapping with the same landmass extent used for the

SDMs and excluded marine IBAs and IBAs on small, remote islands. This resulted in 10176 out of the available 12315 IBA polygons being included in the analysis.

4.3.1 Turnover of species communities within IBAs

For the calculation of turnover values for the different IBAs I used predicted suitabilities of climate suitability from the SDMs. I make the a priori assumption an IBA had the same climate as the cell, or series of half degree cells, within which it is located. Although fine-scale climate data have been produced globally, it has been questioned whether the method used (change-factor method;(Wilby & Wigley, 1997)) actually provides reliable data (Baker *et al.*, 2016). In fact, even using regional climate models (RCMs) to provide future climate projections, climatologists are very cautious of down-scaling projections below circa 25km^2. Here, we use only GCM projections and hence use climate projections at a 0.5^o resolution for most species, so associate climate data at the same resolution with the IBAs. This approach is likely to represent the climate adequately for IBAs in areas with little elevational range, but might be a poor surrogate in mountainous areas, or in other situations when the IBA climate is very different from the surrounding environment (Baker *et al.*, 2015).

I calculated the turnover of species within each IBA between the current (t_1 = baseline (1960 – 1990) and future time period (t_2 = 2041 - 2060) using the Bray-Curtis index of dissimilarity between two communities (Bray & Curtis, 1957), as:

Eqn. 5.1:

$$T_j[t] = \frac{\sum_{k=1}^{s} |P_{jk}\,[t_2] - P_{jk}[t_1]|}{\sum_{k=1}^{s} P_{jk}\,[t1] + \sum_{k=1}^{s} P_{jk}[t_2]}$$

where, P_{jk} = the weighted suitability of species k, t1 = baseline, t2 = future and j = species turnover between the baseline (t1) and future (t2). The turnover values returned are between 0 and 1, with 0 representing no change between the current and future community and 1 indicating a complete changeover between the current and future community composition. The Bray-Curtis index is commonly used as a measure of dissimilarity between communities (Hole *et al.*, 2011; Baker *et al.*, 2015). The turnover is measured relative to the current community composition, high turnover values are thus more likely to occur in species poor areas due to the influence a small number of species can have on the turnover value.

4.3.2 Adaptation Management Strategies

I categorized the IBAs into one of five management adaptation categories, which would facilitate the anticipated community changes within an IBA. I largely followed the methods of Hole et al (2011),

grouping the IBAs based on the number of species projected to colonize to and emigrate from each IBA. To do this, I plotted the proportion of species projected to emigrate from an IBA against the proportion projected to colonize that IBA, and plotted each terrestrial IBA as an individual point. I used the median, lower quartile and upper quartile of values of emigrants and colonists (from across all terrestrial IBAs) to divide the data points into five different sectors: high persistence, increasing values, high turnover, increasing specialisation and increasing diversification (Figure 4.1).

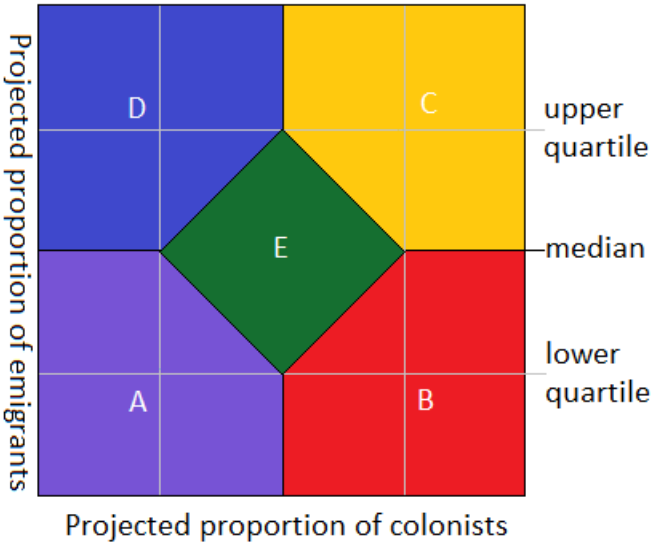


Figure 4.1: Classifying IBAs into adaptation management categories based on the proportion of emigrants and colonists projected between the present and a future period. The classification is based on the median, upper quartile and lower quartile values as illustrated. Management categories are: high persistence (A, purple), increasing value (B, red), high turnover (C, yellow), increasing specialisation (D, blue) and increasing diversification (E, green).

The method I used differs from Hole *et al.* (2011) because instead of using thresholded values for the suitability of the IBA for a species I derive the proportion of emigrants and colonists from the continuous modelled suitabilities. Using the continuous data rather than thresholded values means that the results are not sensitive to the choice of a threshold, which is used to transfer the suitability data to presence or absence values.

4.3.3 Current and future (2050) coverage of terrestrial birds by IBAs

To extract data on range overlap between current and future periods I thresholded continuous suitability data from SDMs to produce binary predictions of suitable/unsuitable. For this, I used the kappa statistic (Cohen, 1960) and chose a threshold that maximised kappa, as described in Chapter 3.

Using the thresholded climate suitabilities derived from the SDMs, I calculated the number of IBAs with which a projected species range overlapped, and the total area of the IBAs with which a species

range intersected, using the 'intersect' tool of the raster package (Hijmans, 2015) and the 'areaPolygon' tool of the 'spatial' package (Karney, 2013). This exercise was conducted for the current period and for 2050, the latter under the medium emission pathway rcp45. The total area of IBA coverage represents the maximum possible area of protection for a species, since the climate suitability of a cell only indicates that the species is likely to be present within a cell but not its distribution within the cell. For each species, I considered both the number of IBAs and the area of those IBAs that intersected with its range, since these two do not necessarily correlate (Supplementary Material Chapter 3, Figure S3.1).

I extracted IBA overlap for 9,071 of the 9,196 species. I had to exclude 125 species which overlaid with corrupted shapefiles. Time limitations precluded fixing or replacing the corrupted shapefiles in the provided IBA dataset.

To identify trends across all species by 2050, I divided the species into groups based on the number of IBAs they are projected to occur in currently and in future. The groups were 'Never represented' for species that are not covered by an IBA both currently and in future, 'Not represented in future' for species that are currently represented but will move out of the IBA network in future, 'Loss of cover' for species that will lose >5% of their current coverage in future, 'Same cover' for species that will have the same coverage +/- 5% in future and 'Gaining cover' for species whose current coverage will increase >5% in future.

GAP analysis

I use the number of IBAs a species range overlaps with to identify 'gap species'. I considered a species to be covered if its projected range overlaps with an IBA to any extent (Rodrigues *et al.*, 2004a; Venter *et al.*, 2014). I compared the number of species projected, using this approach, to be currently protected by the network with the number of species projected to be covered in future, to compare current and potential future 'gaps' in the network.

4.4 Results

4.4.1 Turnover of species communities within IBAs

I calculated turnover values for 10,179 IBAs. The median turnover across all IBAs was 0.53 (Figure 4.2, Figure 4.3). Overall, the spread of turnover values among IBAs within the different biological realms were similar, all comprising areas where the IBAs have a low turnover of species as well as IBAs with high species turnover (Figure 4.2). Regions with several IBAs with high projected turnover include the west coast of North America (Figure 4.4), the Amazon (Figure 4.5), parts of southern Europe, especially Spain, and areas along the Mediterranean Sea (Figure 4.6), the Northern Palearctic (Figure 4.7) and central Australia (Figure 4.9). Areas with low turnover within their IBAs include parts of west and central Africa, including Chad, Sudan and the Central African Republic (Figure 4.8), the Indian subcontinent (Figure 4.9) eastern China (Figure 4.7) and parts of South East Asia (Figure 4.9), especially larger islands such as Borneo and Java. Areas that contain mainly IBAs with intermediate turnover projected occur in southern South America, including Argentina and Chile (Figure 4.5), the western Palearctic (Figure 4.6) and East Africa (Figure 4.8).

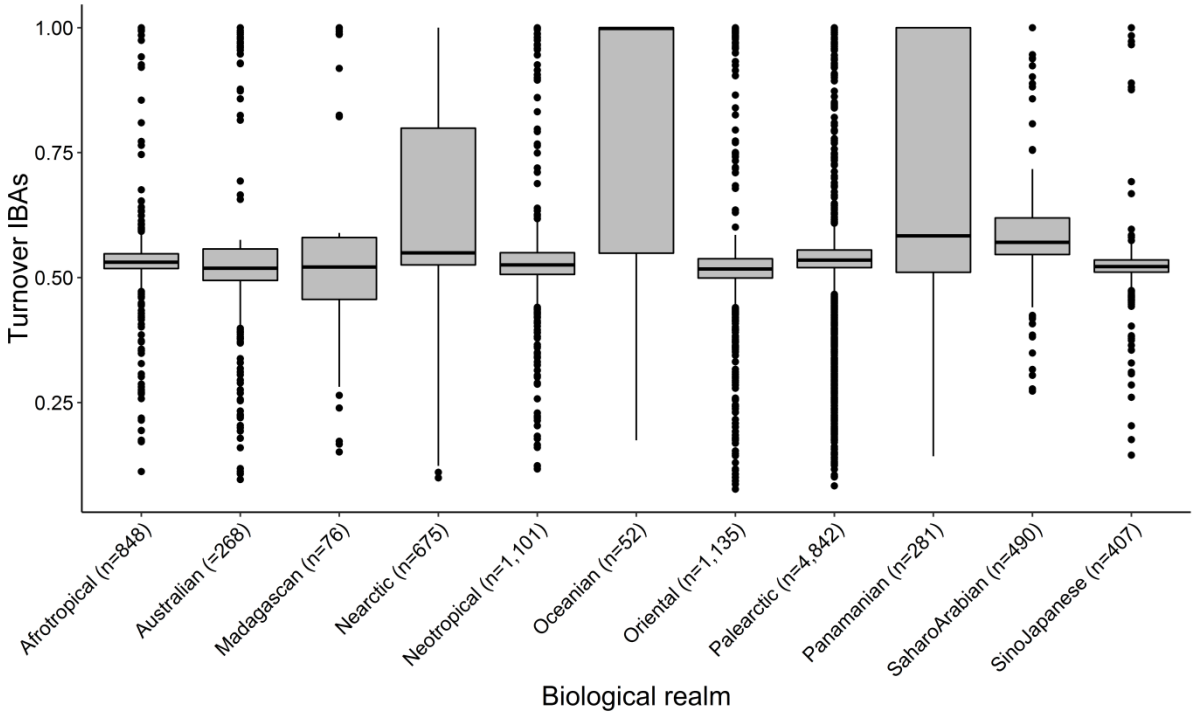


Figure 4.2: Turnover values for the Important Bird and Biodiversity Areas (IBA) across the 11 biological realms (Holt et al. 2013). (for realm map see Chapter 3, Figure 3.1)

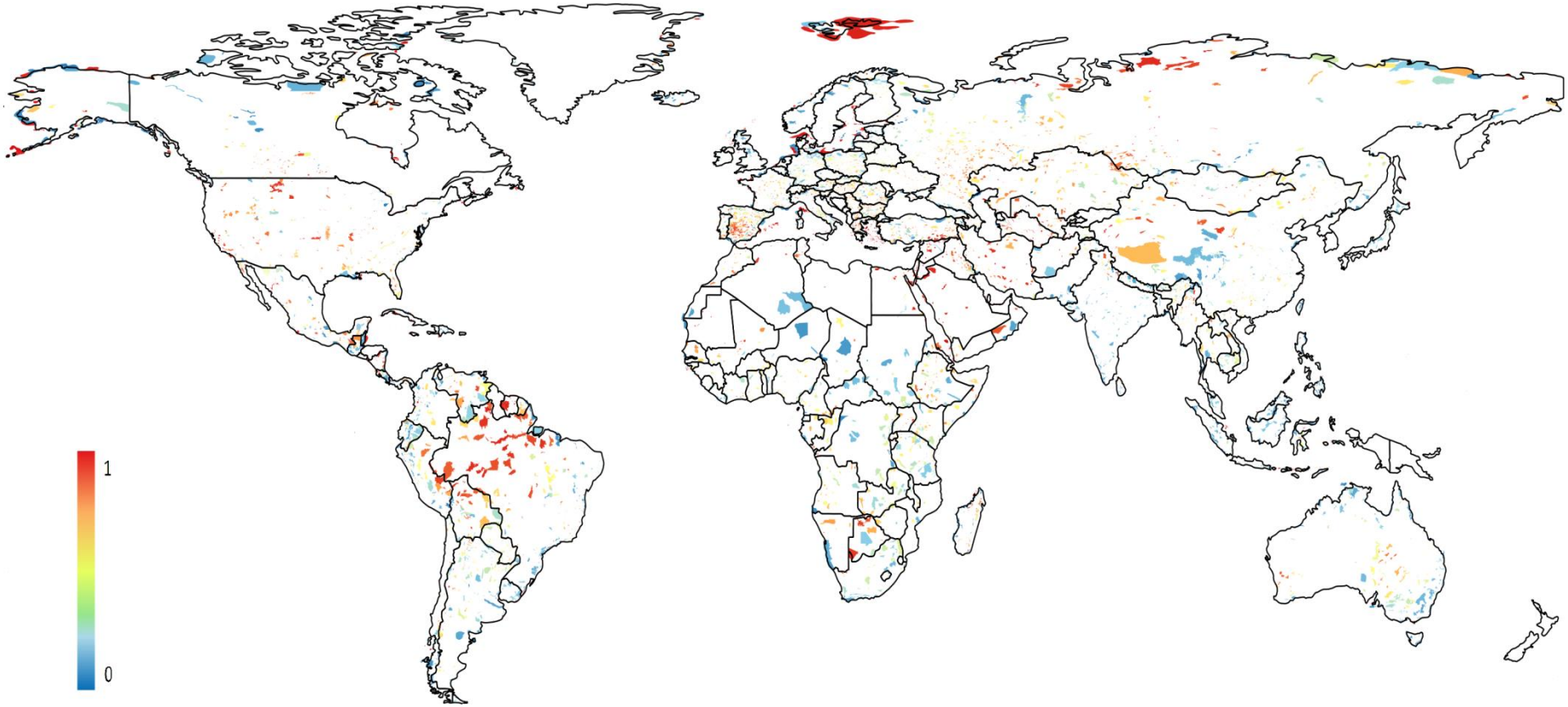


Figure 4.3: Species turnover for each IBA between the current and future period. Blue shading indicates a very low turnover, meaning that the community within the IBA remains very similar. Red indicates a very high turnover, i.e. a near-complete community change by 2050.

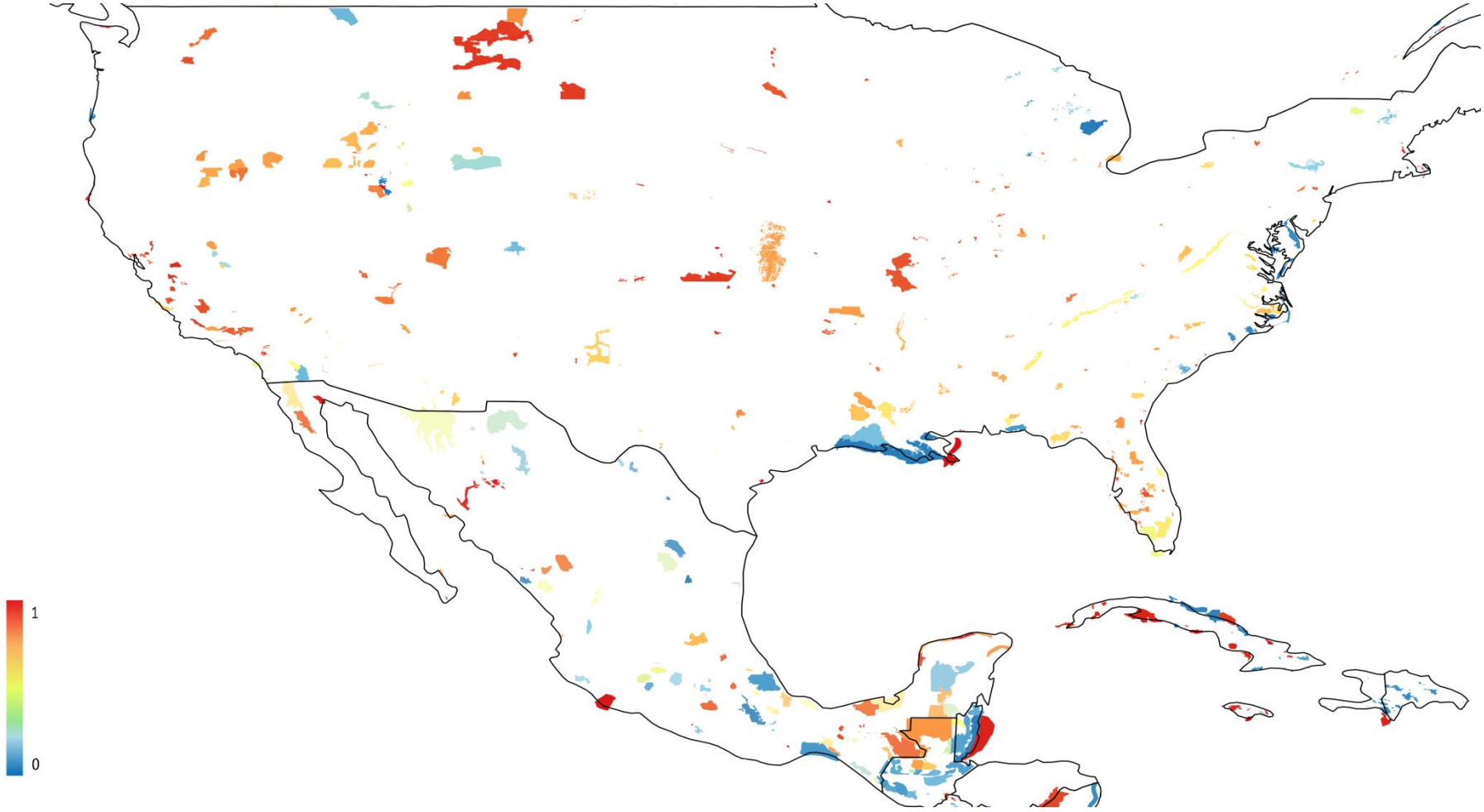


Figure 4.4: Subset map for North America: Species turnover for each IBA between the current and future period. Blue shading indicates a very low turnover, meaning that the community within the IBA remains very similar. Red indicates a very high turnover, i.e. a near-complete community change by 2050.

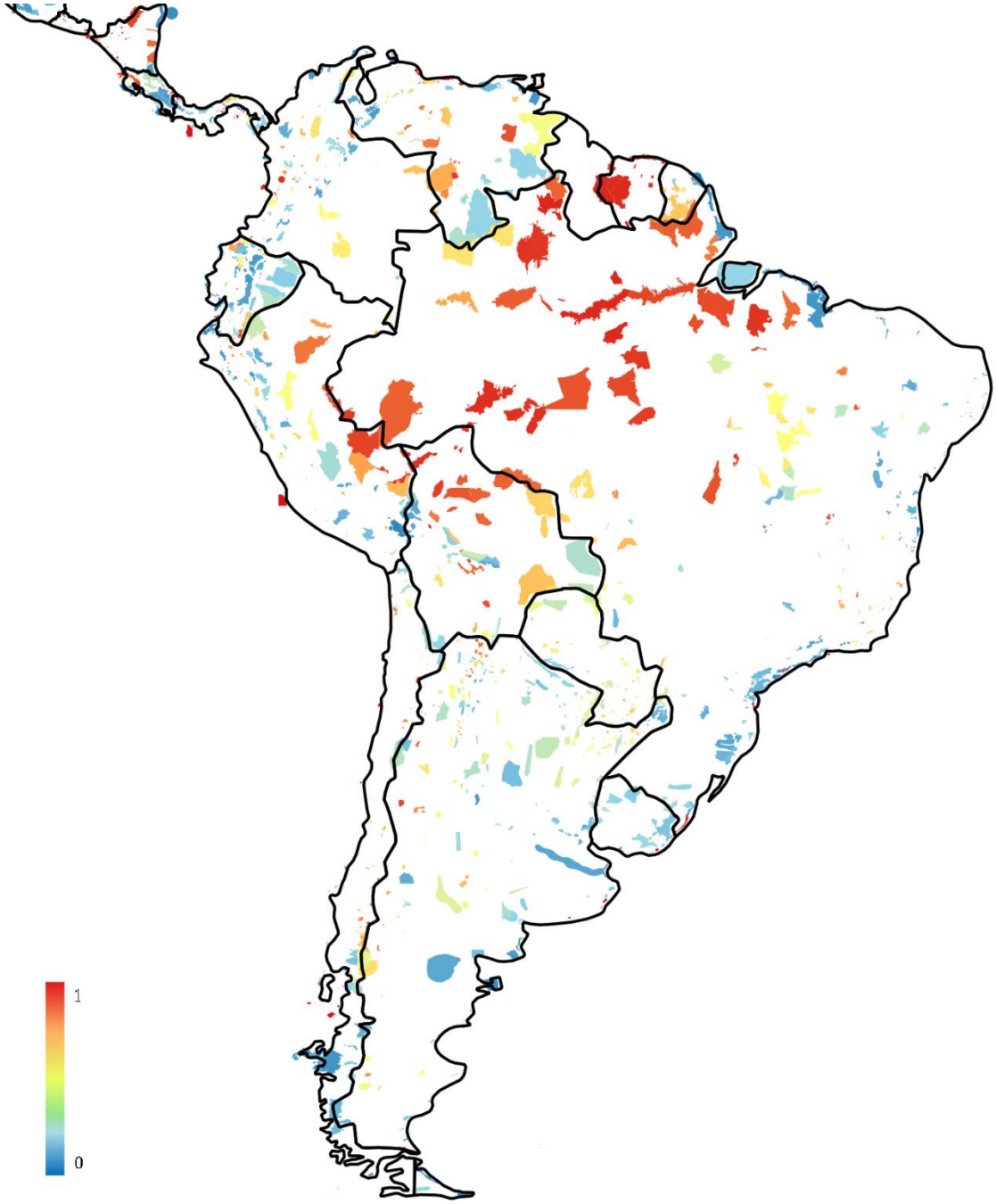


Figure 4.5: Subset map for Central and South America: Species turnover for each IBA between the current and future period. Blue shading indicates a very low turnover, meaning that the community within the IBA remains very similar. Red indicates a very high turnover, i.e. a near-complete community change by 2050.

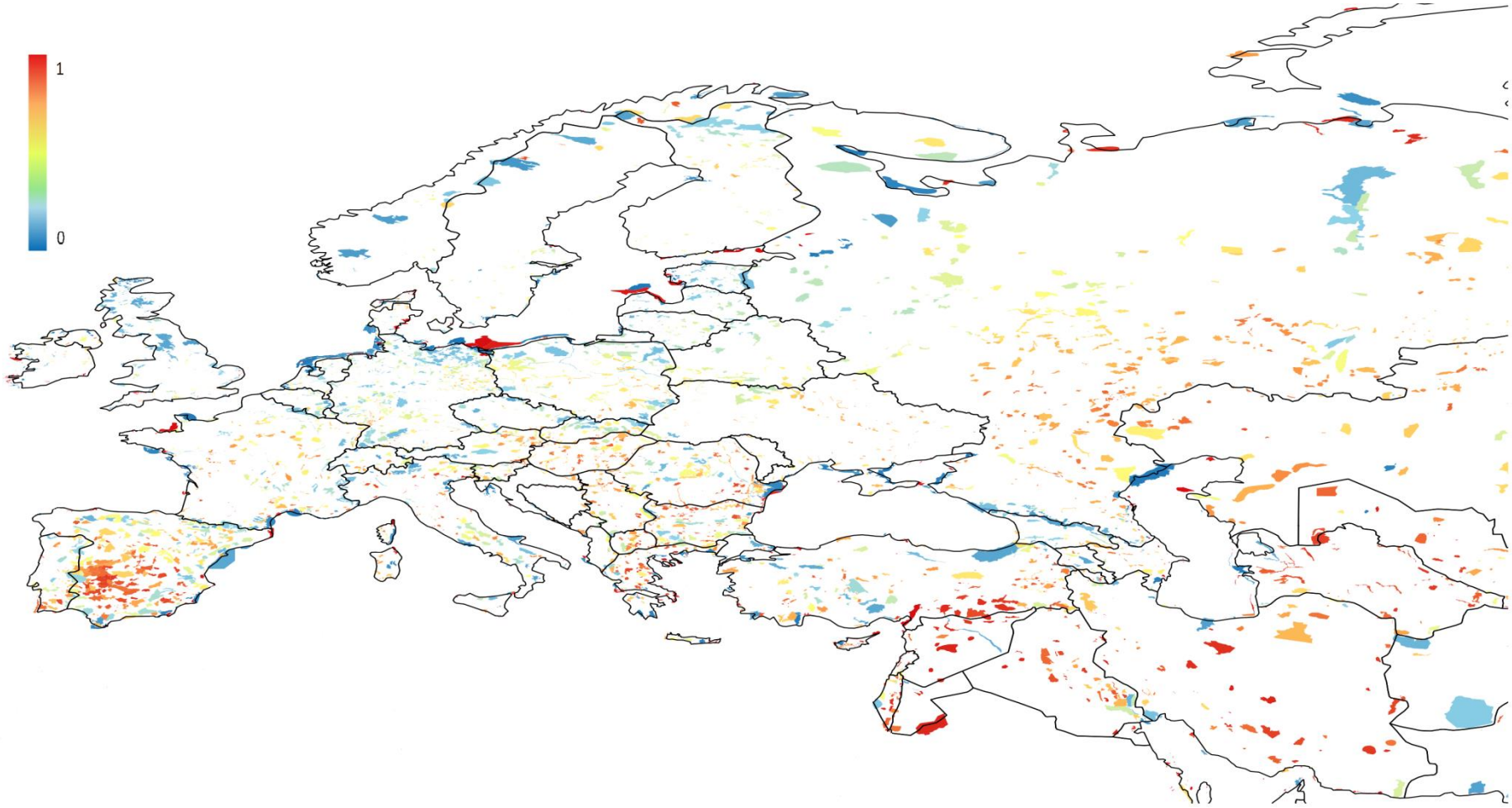


Figure 4.6: Subset map for Africa and the Eastern Palearctic: Species turnover for each IBA between the current and future period. Blue shading indicates a very low turnover, meaning that the community within the IBA remains very similar. Red indicates a very high turnover, i.e. a near-complete community change by 2050.

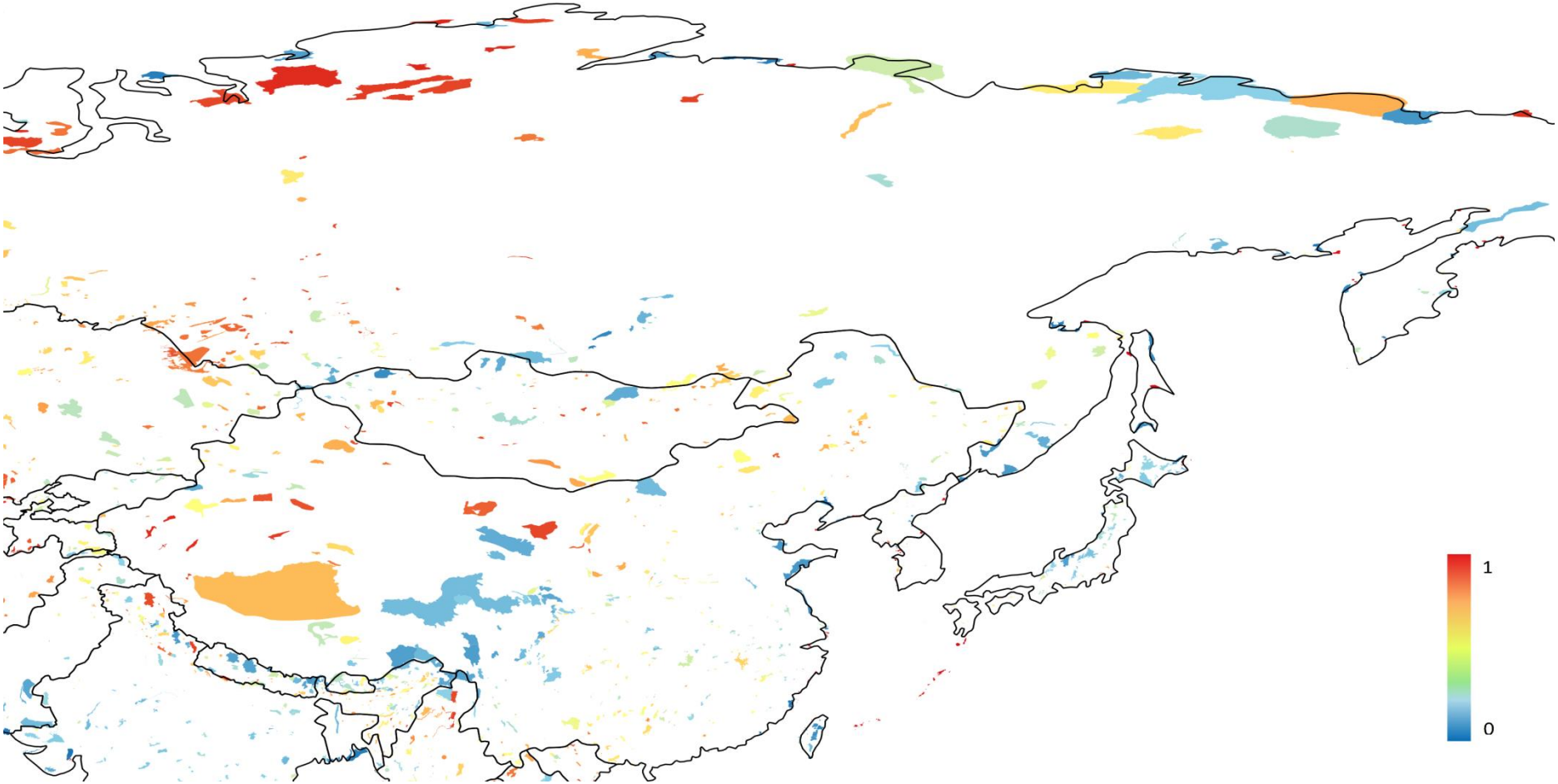


Figure 4.7: Subset map for Asia: Species turnover for each IBA between the current and future period. Blue shading indicates a very low turnover, meaning that the community within the IBA remains very similar. Red indicates a very high turnover, i.e. a near-complete community change by 2050.

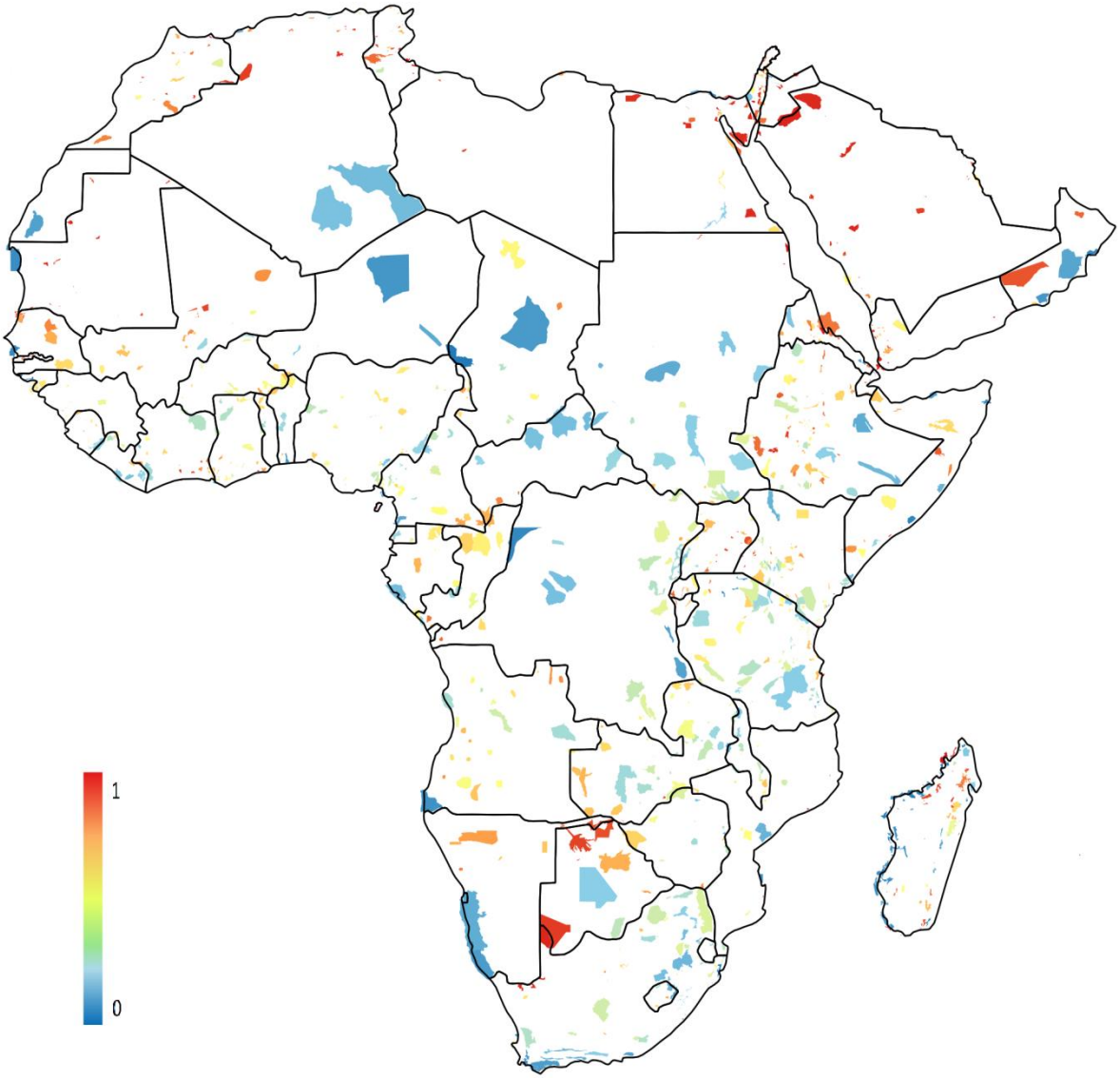


Figure 4.8: Subset map for Africa: Species turnover for each IBA between the current and future period. Blue shading indicates a very low turnover, meaning that the community within the IBA remains very similar. Red indicates a very high turnover, i.e. a near-complete community change by 2050.

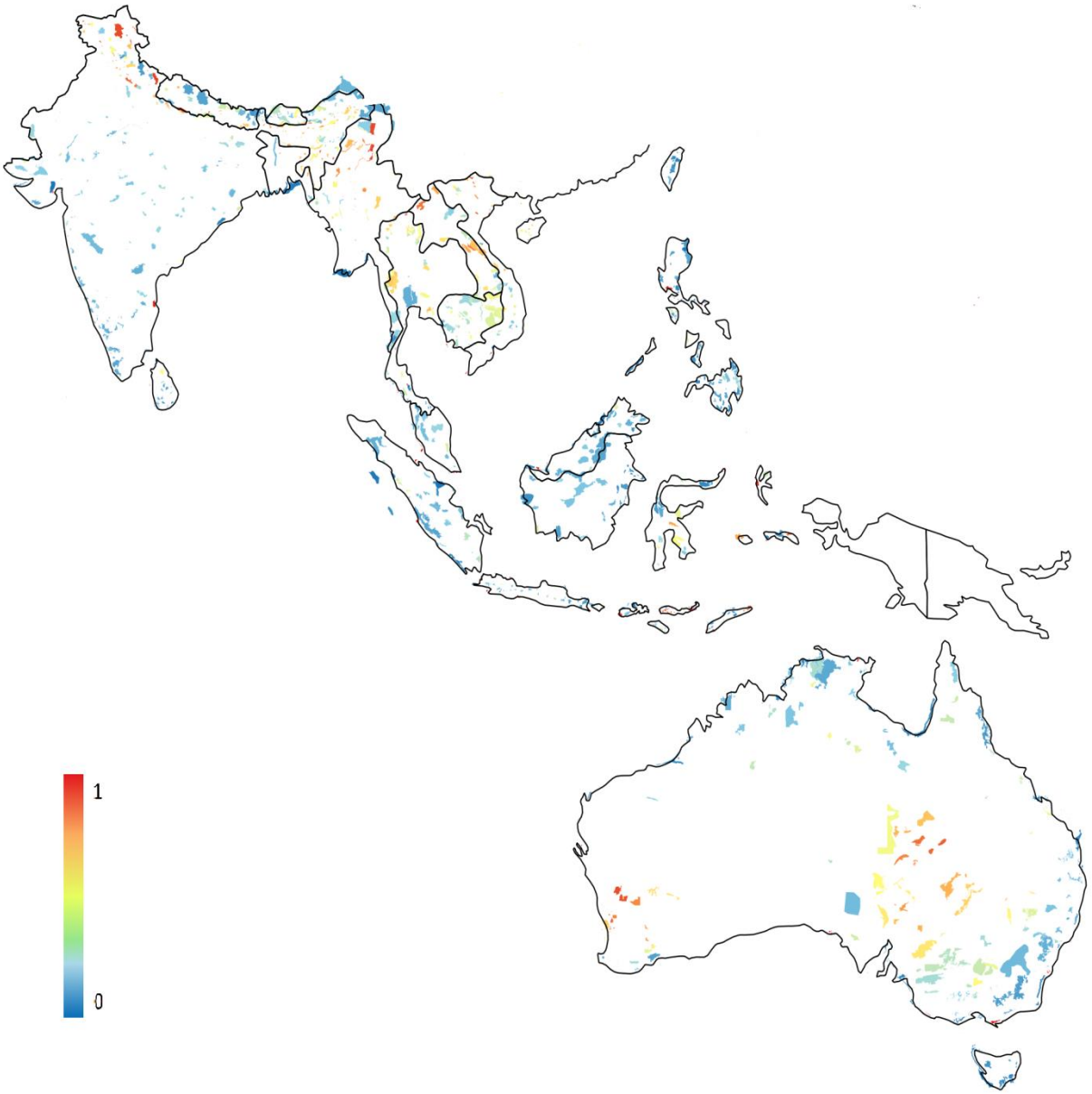


Figure 4.9: Subset map for India, South East Asia and Australia: Species turnover for each IBA between the current and future period. Blue shading indicates a very low turnover, meaning that the community within the IBA remains very similar. Red indicates a very high turnover, i.e. a near-complete community change by 2050.

4.4.2 Climate change adaptation categories

The median proportion of emigrants (0.67) per IBA was greater than the projected colonists (0.06). Of the 10,176 IBAs included in the analysis 1,485 were classed as 'High persistence', 2,683 as 'Increasing value', 1,630 as 'High turnover', 2,741 as 'Increasing specification' and 1,637 as 'Increasing diversification' (Figures 4.10 and 4.11).

The climate change adaptation categories calculated for IBAs mirror, to a large extent the turnover values, as might be expected given that they are both derived from the numbers of predicted colonists and emigrants. The IBAs in the 'High turnover' management categories also tended to have the highest turnover values (Supplementary material Chapter 4, Figure S4.1). However, the two summary statistics are not direct parallels. For example, IBAs with high turnover located along the Westcoast of North America (Figure 4.4 and 4.12), in the Amazon (Figure 4.5 and Figure 4.13) and central Australia (Figure 4.9 and 4.17) areas are mainly classified as 'High turnover' management category but many are also classified as 'Increasing diversification' as a result of the high proportions of emigrating species in these areas. IBAs with high turnover in parts of Southern Europe, especially Spain and areas along the Mediterranean Sea (Figure 4.6 and 4.14) as well as the Northern Palearctic (Figure 4.7 and Figure 4.15) typically fall into the management categories of 'High turnover' or 'Increasing value', as a result of high proportions of colonising species in these areas. IBAs with low turnover in central Africa including Chad, Sudan and the Central African Republic (Figure 4.8 and Figure 4.16), the Indian subcontinent (Figure 4.9 and Figure 4.17) eastern China (Figure 4.7 and 4.15) and parts of South East Asia (Figure 4.9 and 4.17), are mainly classified as 'High persistence'.

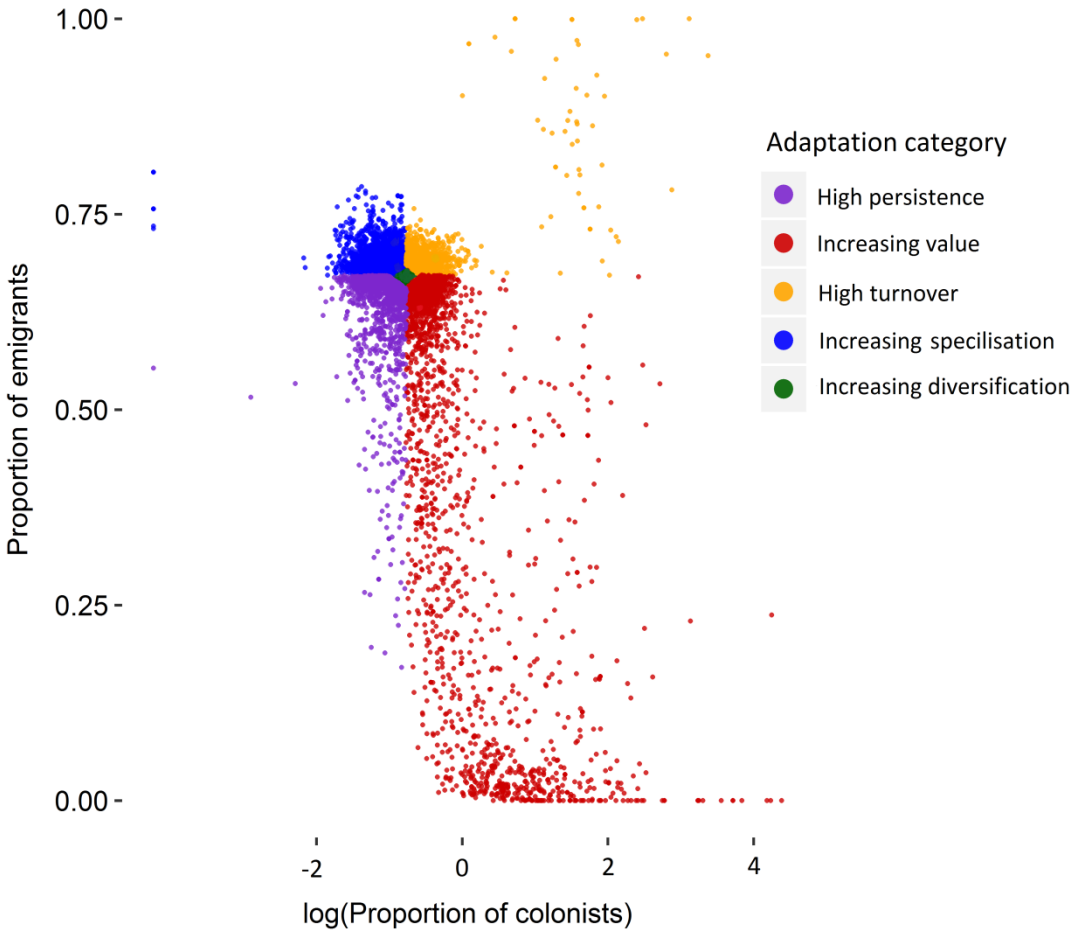


Figure 4.10: Proportion of bird species predicted to emigrate from an Important Bird Area (IBA) against the proportion of bird species predicted to immigrate into and IBA by 2050. The colours are according to the climate change adaptation category the IBA falls into.

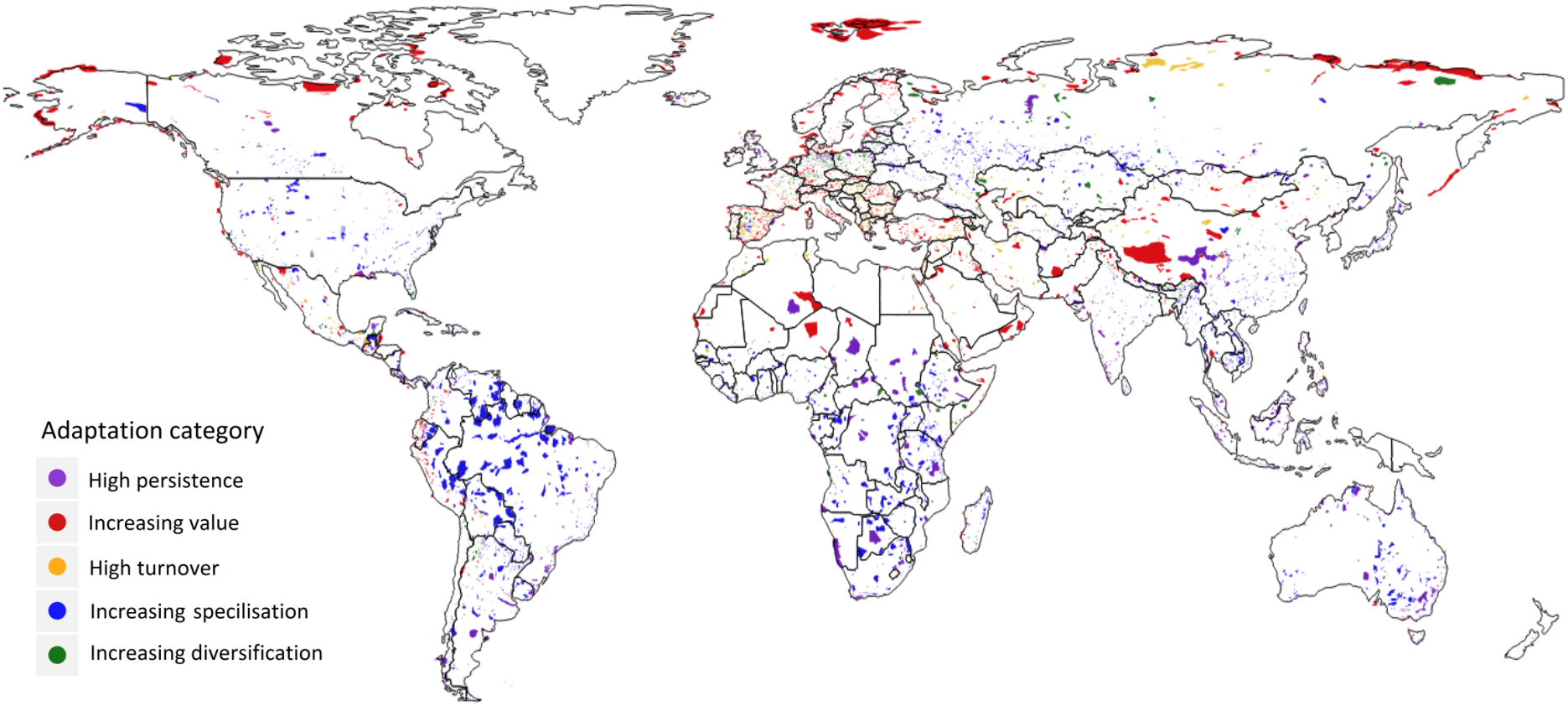


Figure 4.11: The spatial distribution of the global Important Bird and Biodiversity Areas (IBAs) and the climate change adaptation class each IBA falls into.

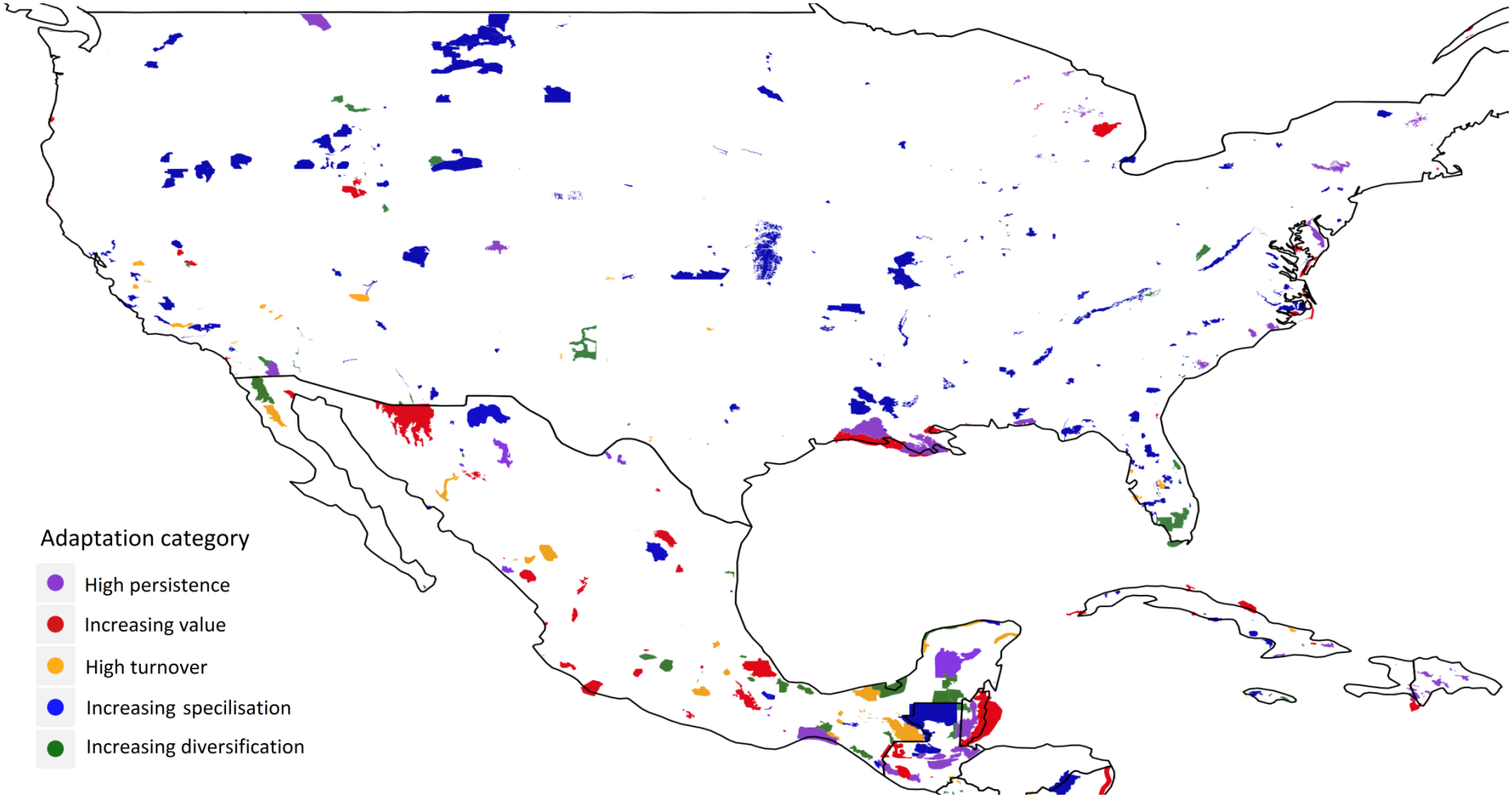


Figure 4.12: Subset map for North America: Spatial distribution of the global Important Bird and Biodiversity Areas (IBAs) and the climate change adaptation class each IBA falls into.

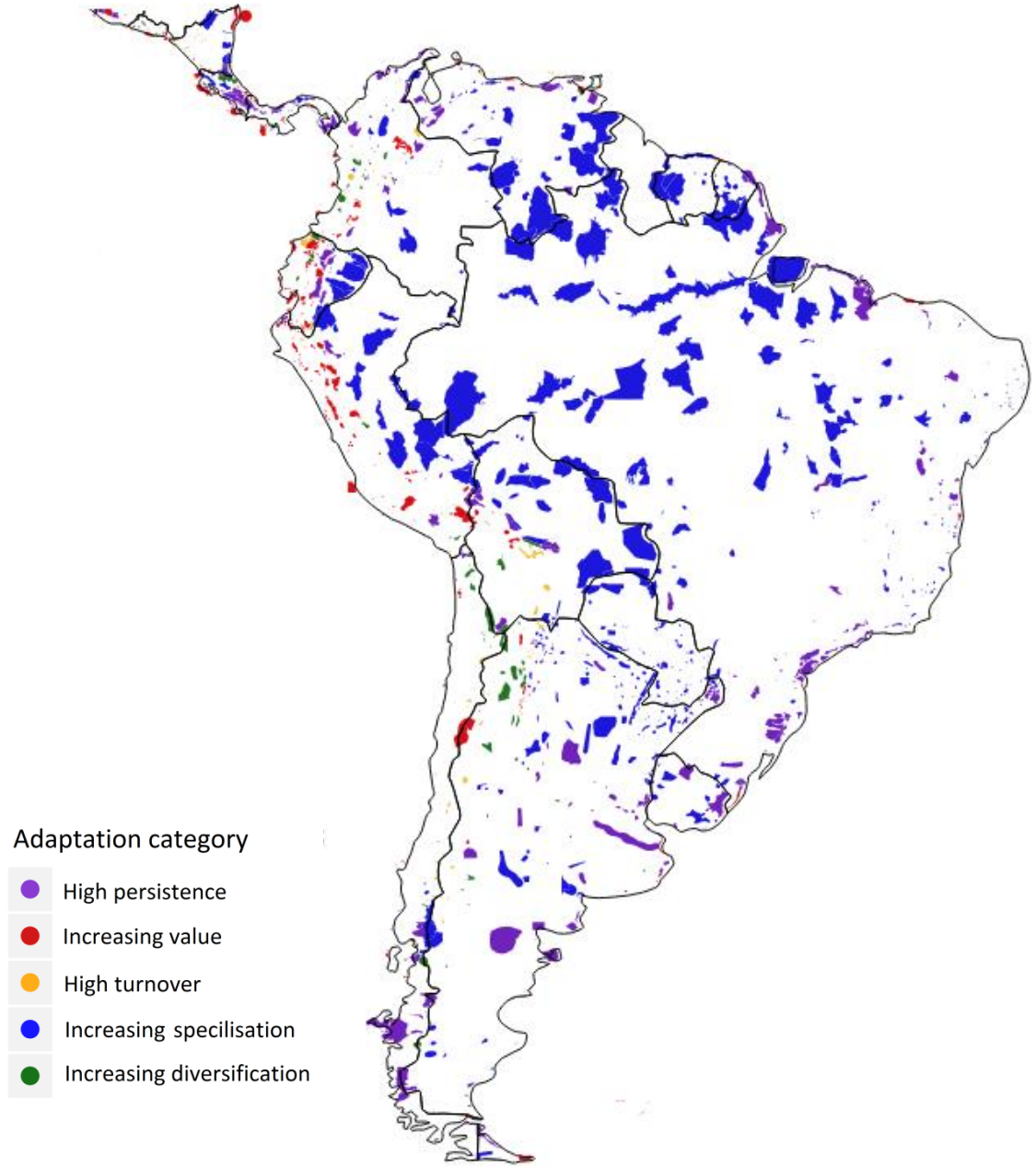


Figure 4.13: Subset map for South America: Spatial distribution of the global Important Bird and Biodiversity Areas (IBAs) and the climate change adaptation class each IBA falls into.

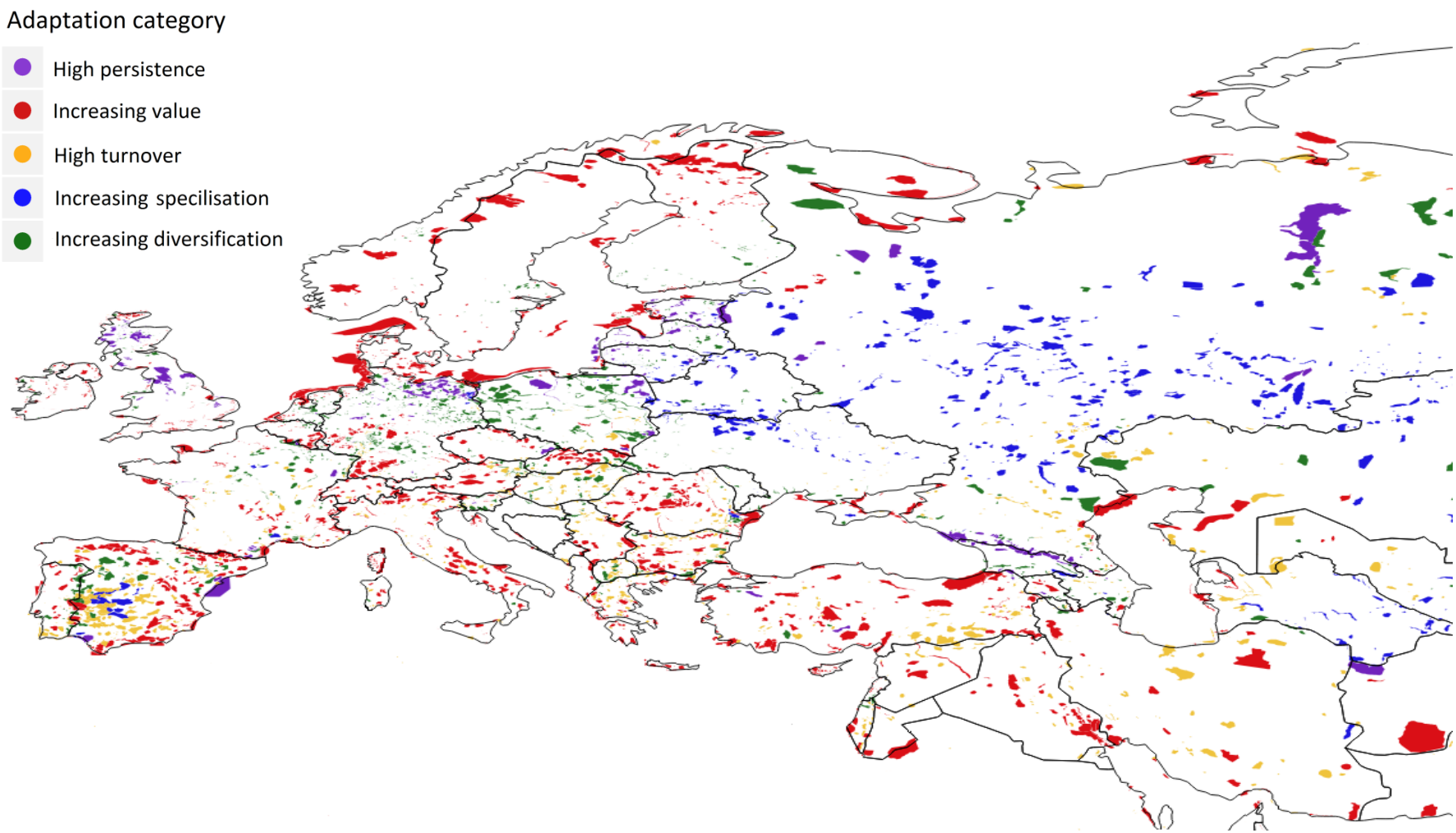


Figure 4.14: Subset map for Europe: Spatial distribution of the global Important Bird and Biodiversity Areas (IBAs) and the climate change adaptation class each IBA falls into.

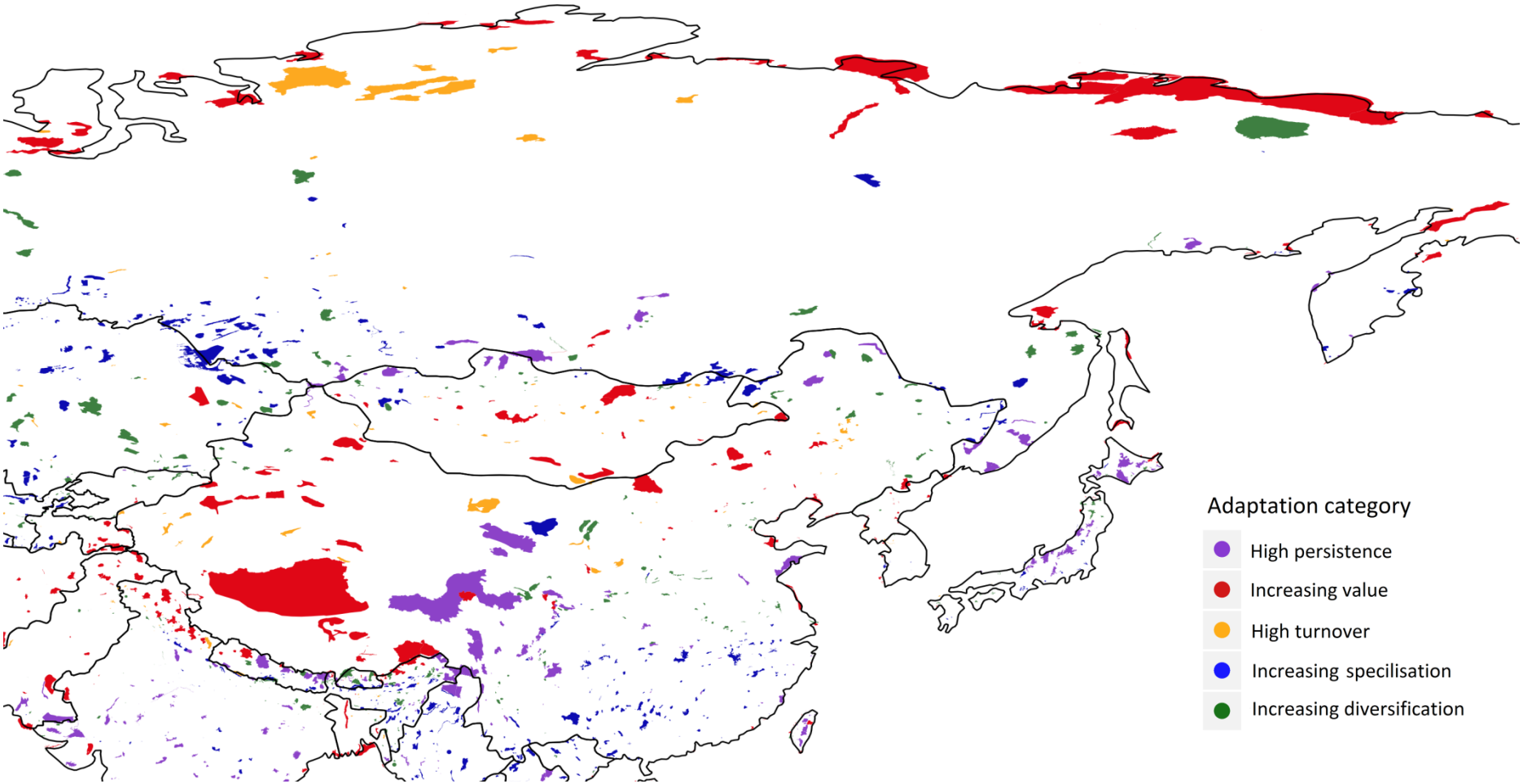


Figure 4.15: Subset map for Asia Spatial distribution of the global Important Bird and Biodiversity Areas (IBAs) and the climate change adaptation class each IBA falls into.

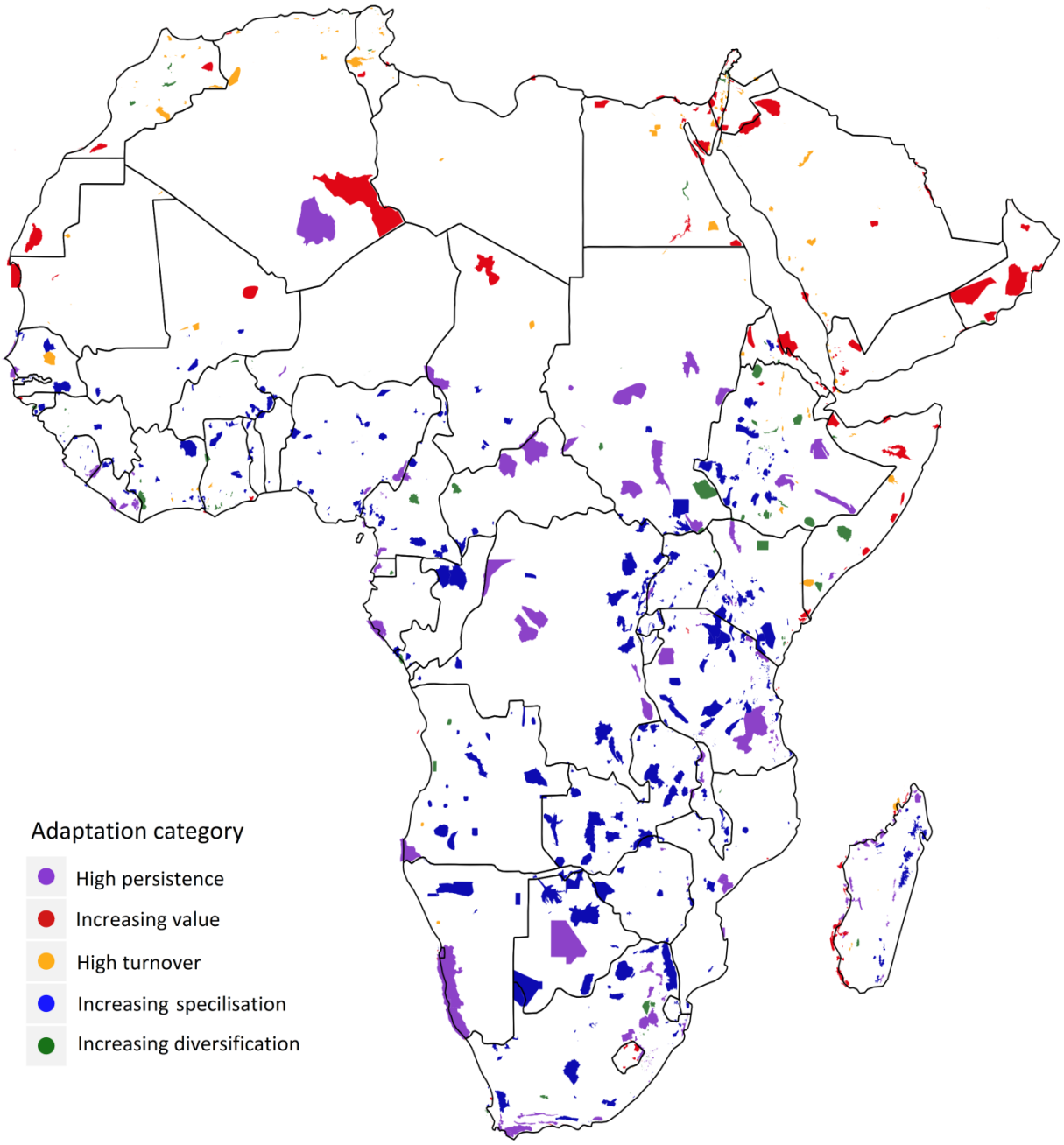


Figure 4.16: Subset map for Africa: Spatial distribution of the global Important Bird and Biodiversity Areas (IBAs) and the climate change adaptation class each IBA falls into.

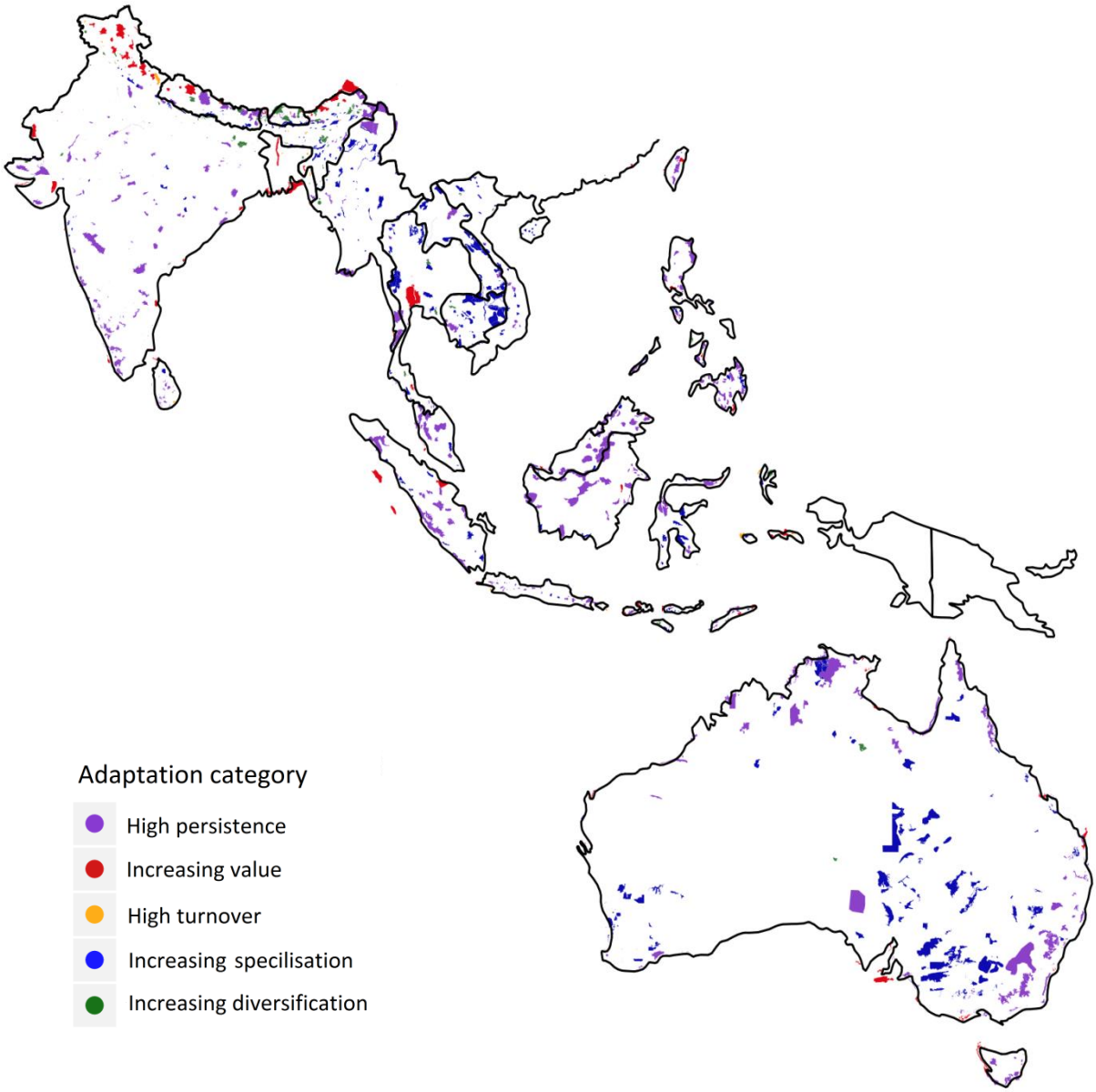


Figure 4.17: Subset map for India, South East Asia and Australia: Spatial distribution of the global Important Bird and Biodiversity Areas (IBAs) and the climate change adaptation class each IBA falls into.

4.4.3 Species coverage by the IBA network

I extracted the number of (IBAs) in which each species was projected to occur, both currently and by 2050, for 9,071 species. Overall, more species are projected to decline in IBA representation (4,319 species) in future than to increase in representation (2,431 species; Figure 4.18 a & b). The area of IBA and range overlap (in km^2) currently and in the future (2050) was calculated for 8,821 species. The IBA overlap in km^2 for each species shows a similar pattern of change in the future to the representation results, with more species losing cover (5,995) than gaining cover (2,013; Figure 4.18 c & d).

267 species are projected not to have any range that is covered by the IBA network (current GAP species) at present, and 1,043 species that are projected to be occur in IBAs at present are projected to lose their coverage by 2050 (future GAP species). Of these futures GAP species, 732 are projected to have no suitable climate simulated anywhere in future and 311 have suitable climate in regions outside of the IBA network (Figure 4.19 b). The majority of the 267 species that have no current IBA coverage (Figure 4.19 a) are located in Papua New Guinea (which has no IBAs designated), though a few of these species also occur in the Amazon region, the northern Palearctic and southern Africa.

Highlighting species that do not qualify as GAP species but which are nonetheless projected to experience substantial loss in IBA coverage indicates that the majority of these species are located in the Amazon region, with others occurring in the Palearctic. Species with the highest loss in IBA coverage (> 75%) are mainly located in the Amazon (Figure 20 a). Species projected to lose ≥50% to 75% of their IBA coverage include many species in the northern Palearctic (Figure 4.20 b).

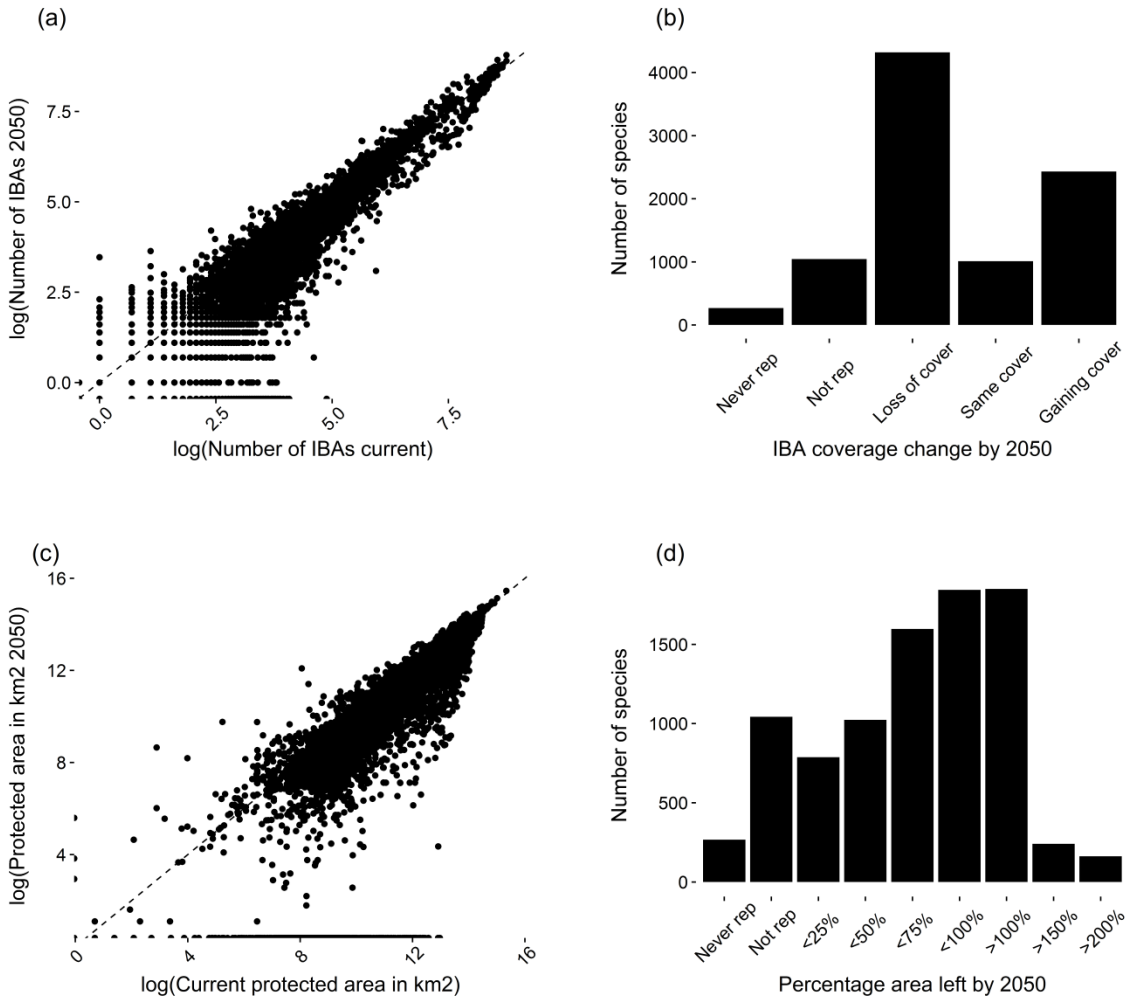


Figure 4.18: Changes in (a) number of IBAs and (c) their areal extent for individual species between the present and 2050. (b) Number of species (n=9071) that are not currently represented in an IBA (GAP species, 'Never rep'), the species that will not be represented in an IBA by 2050 ('Not rep') and the number of species that are losing and gaining IBA coverage. (d) the percentage change in area of a species range that is protected within an IBA in the future, relative to its current area of IBA protection (n=8,821).

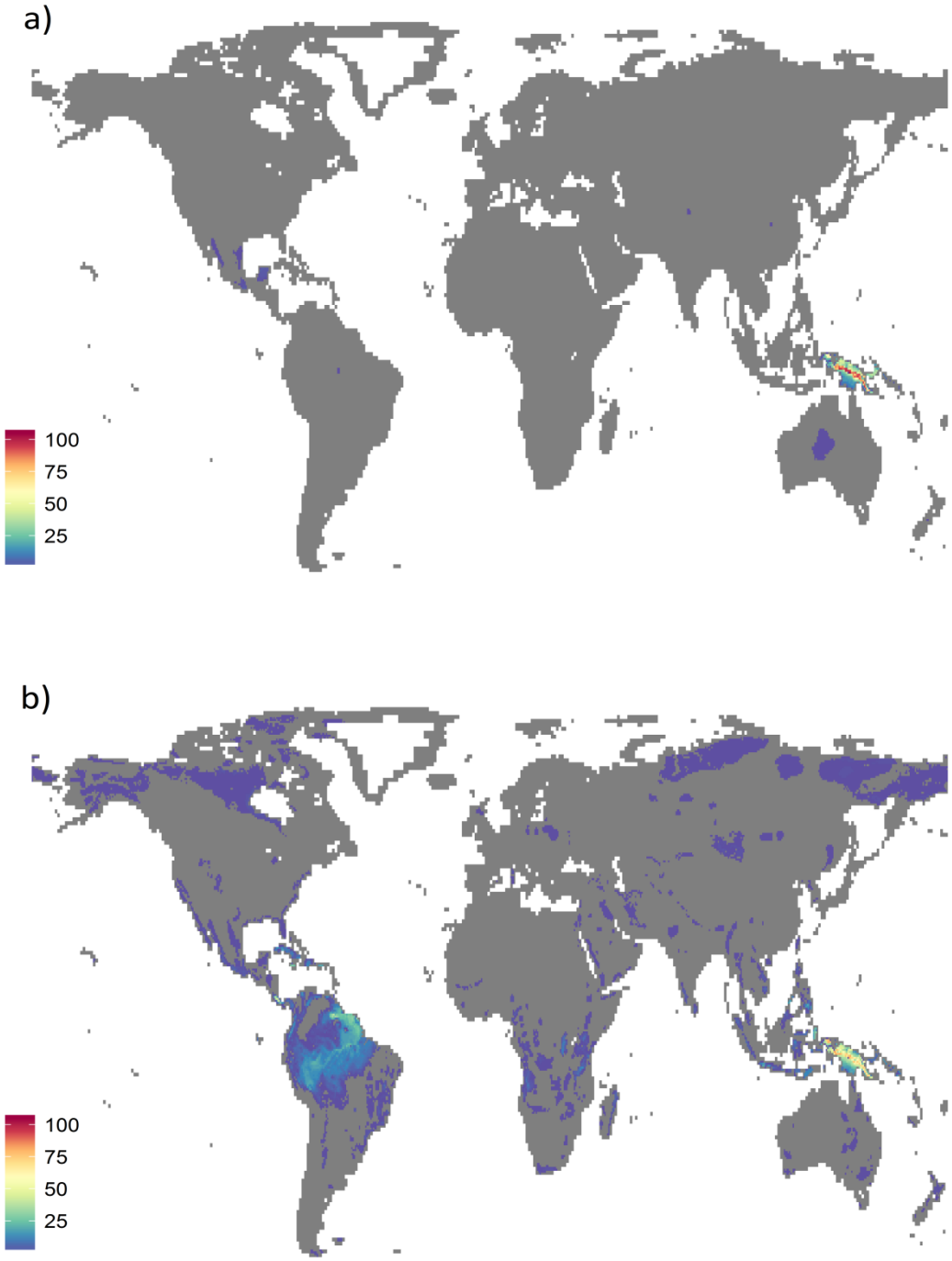


Figure 4.19: GAP analysis showing (a) the current richness of species that are not covered by the IBA network at present and (b) species that are projected to have no IBA coverage by 2050 (excluding species that are predicted to lose all climatically suitable range by 2050).

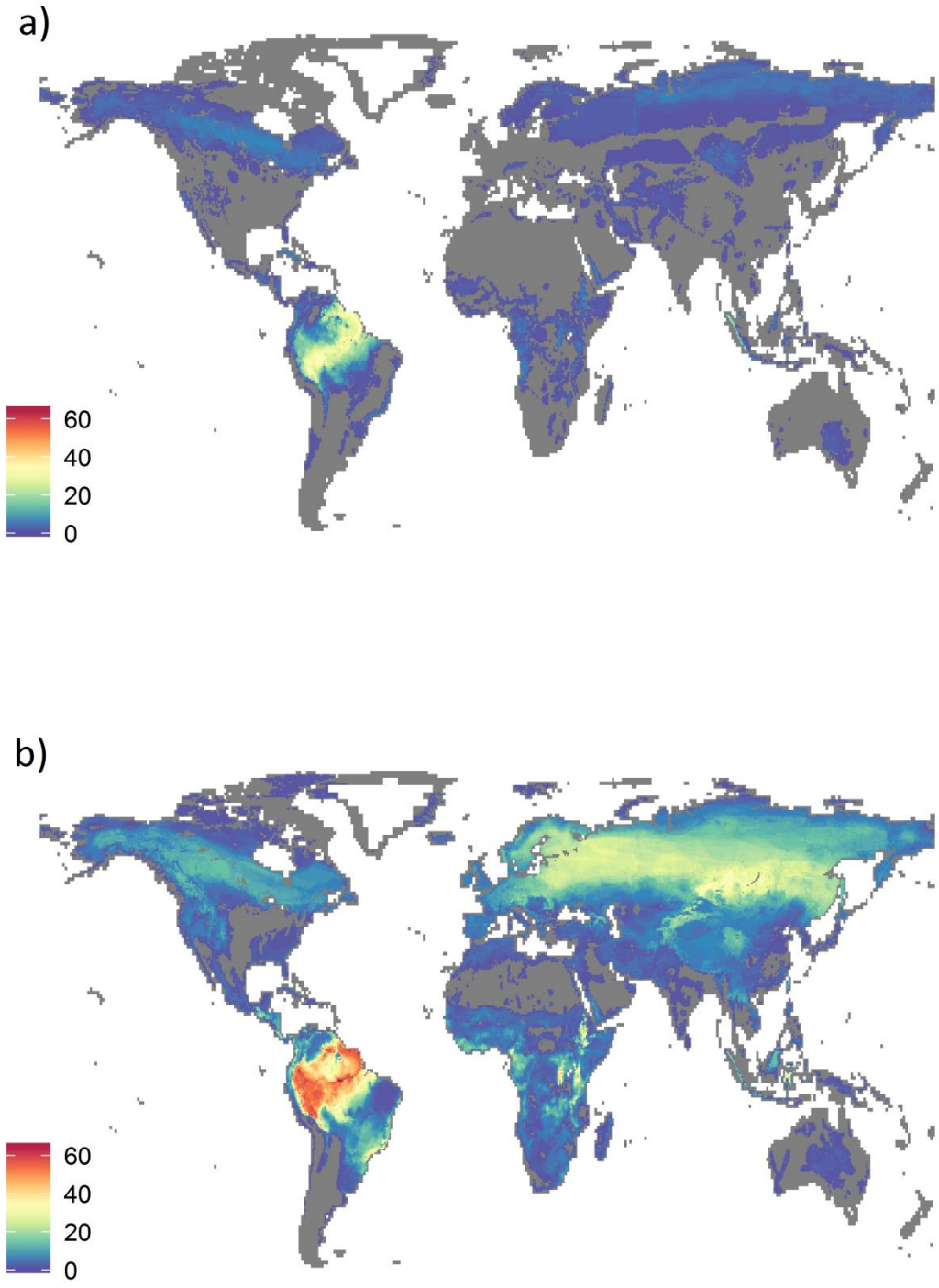


Figure 4.20: Current distribution of those species that are (a) predicted to lose more than 75% of their IBA coverage and the current distribution of species that will (b) lose between 50% to 75% of their IBA coverage.

4.5 Discussion

The geographic distribution of areas that are most important for conservation is likely to change under climate change (Lee & Jetz, 2008). Earlier studies have suggested changes in the importance of PAs across networks, with some sites gaining value and others becoming redundant for species conservation in the long term. Sites might also become important in the short term, e.g. as stepping stones facilitating species movements, despite not retaining their importance in the long term (Araújo *et al.*, 2004; Hannah *et al.*, 2007; Bagchi *et al.*, 2013; Alagador *et al.*, 2014). These projected temporal changes highlight the importance of understanding how PA networks are affected by range changes under climate change and to incorporate these projected range changes to facilitate movements across PAs and optimise the coverage of the PA network (Hannah *et al.*, 2002; Hannah & Hansen, 2005). In this chapter, I have investigated the impact of projected range changes in terrestrial birds on their protection by the global IBA network and provided a first overview of where impacts are projected to be highest and how the coverage of terrestrial bird species by the network is changing. Overall, the coverage provided is decreasing, with a clear spatial pattern of IBAs that are projected to be stable, in terms of their species communities, and areas projected to undergo major changes.

4.5.1 Species turnover within IBAs

There is a clear spatial patterning in projected turnover, with IBAs with high turnover being located in the Amazon, as well as parts of Southern Europe, especially Spain and areas along the Mediterranean Sea and the Northern Palearctic. These areas of high turnover are in agreement with other studies on observed and projected range changes of species moving north (Thomas & Lennon, 1999; Virkkala *et al.*, 2008; Virkkala & Lehikoinen, 2014) leading to higher fluctuations in protected areas in the northern Palearctic (Virkkala *et al.*, 2013; Santangeli *et al.*, 2017), and projected colonisation of North African migrant species into areas north of the Mediterranean Sea e.g. into Spain (Barbet-Massin *et al.*, 2010). The high turnover rates in IBAs located in the Amazon results conform to the results from Chapter 3, predicting high reduction in range extent especially species in the Amazon. An area that stands out with low turnover values is the Andes, given how many montane species might be expected to be incapable of traversing gaps to next nearest mountain range (Grabherr *et al.*, 1994; Williams *et al.*, 2003; Wilson *et al.*, 2005; Sekercioglu *et al.*, 2008; La Sorte & Jetz, 2010). In this region, summed dispersal might produce slightly misleading projections of range changes, given the need to potentially move individual long-steps between sites located on different mountain tops and ranges. Producing an iterative, annual dispersal model might be a useful tool in these areas, to account for natural barriers that species are unlikely to cross.

4.5.2 Adaptation management strategies

Including projected climate change impact into management plans is important to enable conservation managers to make informed decisions (Mawdsley *et al.*, 2009). Grouping protected areas across a network into adaptation management categories, based on changes in their species composition, can help set goals to maximise the long-term values of the individual protected areas (Hole *et al.*, 2011). The global pattern of the assigned climate change adaptation categories largely mirror the turnover values calculated and likewise conform to the above described observed and projected range changes.

The adaptation management category results I produced across Africa can be compared to a previous exercise conducted by Hole *et al* (2011). Whereas Hole *et al* (2011) classified most of the IBAs across Botswana, Mozambique, Zimbabwe, Zambia and Angola as "high turnover" sites; I classified these areas as being mostly of "Increasing specialisation", projecting fewer colonists in this area. Two possibilities could lead to these differences in the predicted management categories. The allocated management category depends on the subset of PAs that is assessed during the analysis. A PA might have a comparably high turnover based on the number of emigrants and colonists when compared to the subset of PAs in Africa but when compared to the global PA network, these changes might be less extreme overall. As there are areas with much higher turnover (e.g. in the Mediterranean, or the Northern Palearctic) than occur in Africa, this could have affected the categorisation. This shows the importance of considering the spatial extent when considering priorities for management and for adaptation planning for conservation purposes. A global extent will highlight patterns in a global context. However, for conservation management purposes, classifying the changes over a smaller extent, as for example by biological realm, might be more applicable Secondly, I incorporated natal dispersal ability into the projections which was not accounted for in the previous study (Hole *et al.*, 2009; Hole *et al.*, 2011). The sites that were previously high turnover, between the savannas of South Africa and Kenya, are now almost all increasing specialisation, as the species cannot make the dispersal movements required. This highlights the difference including dispersal can make to the projections of species ranges and subsequently can affect resulting conclusions drawn for management purposes. The median proportion of colonists for the African IBAs by Hole *et al* (2011) was 0.34. The median proportion of colonists I found across the IBAs is not directly comparable being derived from many more IBAs but, at 0.06, it is an order of magnitude smaller indicating many more areas have fewer colonising species in a global context. This again might be a result of including dispersal ability into the future projections, reducing the number of species that colonise new IBAs, by only allowing them to colonise climatically suitable IBAs within their natal dispersal range.

4.5.3 Changes in IBA coverage and 'GAP species'

Prior regional assessments of the future potential for current PA networks to safeguard biodiversity have all suggested that the overall protection offered by such networks is reduced, though they differ in their extent of the forecast reduction (Araújo *et al.*, 2004; Coetzee *et al.*, 2009; Kharouba & Kerr, 2010; Araújo *et al.*, 2011). The GAP analysis conducted here for bird species across the global IBA network support these regional assessments. The number of species losing IBA representation in future far outweighs those that gain representation.

The current coverage of the IBA network for terrestrial birds, based on our simplifying assumption that climatically suitable areas overlapping with an IBA equate to projected occupancy, is high, with only 267 species simulated as protected by at least one IBA. Many of these species are located on Papua New Guinea which does not have any IBAs at present. For both time points, the overlap of a species' predicted distribution with an IBA is considered as equating to the species being protected. However, this does not necessarily mean that the species is present inside the IBA. Additionally, any overlap was counted, which is a commonly used approach in large scale GAP analysis (Rodrigues *et al.*, 2004a; Venter *et al.*, 2014), but it means that a species being covered by the network in this analysis does not necessarily reflect if enough of the species range is covered to safeguard it under climate change. Notwithstanding these caveats, the overall trend is for species to have more restricted ranges under climate change and, consequently, reduced coverage by the PA network.

Furthermore, the used approach can indicate global spatial patterns and highlight areas that harbour high numbers of species which are projected to move out of the protected area network. These can then be focus for further studies possibly working on a finer scale and incorporating downscaled regional climate data and habitat data setting species specific targets for minimum range cover and suitable habitat, which is computationally intense and impractical on a global scale.
Especially the use of fine-scale modelling and regional climate simulations, should be future priority, since the projection of changes in species ranges based on GCMs can give a good overall indication of large scale patterns but, especially in areas of high relief, potential climate refugia might be overlooked (Austin & Van Niel, 2011; Franklin *et al.*, 2013) and range projections for individual species might be misleading.

Future work

Here, I looked at the coverage provided by an idealized network, which is expected to be high since the aim is to cover global avian biodiversity and many of the sites are not formally protected (BirdLife International & NatureServe, 2017). Nevertheless evaluating its future performance can help identifying the future potential of the individual IBAs. IBAs might become redundant under

climate change as species move out of them and spatial prioritization strategies can be more cost efficient than and optimize conservation effort, rather than maintaining all areas within the network. (Alagador *et al.*, 2014). This is especially true since expanding the IBA network to cover all unprotected and partially protected sites and managing them efficiently is costly and has been estimated to be about $50.7 billion annually (McCarthy *et al.*, 2012).

Future work already underway is undertaking similar analyses for the IUCN PA network, i.e. real network of protected areas (rather than an idealized network) to compare how the projections and 'gaps' differ. Additionally, future work will incorporate global land use change data, with the aim of producing more realistic communities within the protected areas.

The results presented in this chapter followed a very basic approach identifying 'gap species' that are not represented by the IBA network, based on spatial overlap with the IBA polygons (Jennings, 2000). Identifying species not currently covered by the protected area network, gives an indication how complete the cover is that the network provides for biodiversity (Rodrigues *et al.*, 2004a). Comparing present and future coverage allowed confirming the trend of species moving out of protected areas under climate change. Following the incorporation of land use data, I aim, in follow-on work to set targets (in terms of both representation and the areal extent of protection) for species protection and to use an optimization algorithm to identify areas that could complement the network to provide maximum coverage for terrestrial bird species.

Chapter 5:

A first global assessment of the potential of assisted colonisation to aid the conservation of the world's birds under projections of climate change

5.1 Abstract

The principal responses of species to climate change are likely to be spatial changes in range and abundance. Thus, a species' ability to adapt to climate change will depend on its ability to track suitable climate. Adaptive conservation management to mitigate climate impacts on biodiversity often advocates facilitating natural range alterations. However, for species with constrained mobility, assisted colonisation (the artificial translocation of species to suitable areas they are unlikely to reach unaided) has been proposed as a potential conservation tool. Here we use species distribution models (SDMs) to identify climatically suitable areas for almost all terrestrial landbirds, both now and in future. We use these models, along with species' habitat and trait data, to simulate the likelihood that bird species can disperse and track suitable climate and habitat throughout the century. The comparison between a species' current range extent, and the extent of future suitable habitat and climate that lie within its colonisation potential, are used to identify species most at threat from climate change. If such threatened species have suitable habitat and climate beyond their dispersal capability, they could be candidates for assisted colonisation (AC). I use species trait data, including natal dispersal range, feeding guild, generation length, current range extend and mean latitude of occurrence, to identify attributes that make a species more likely to be an AC candidate. Using this approach, I summarise, for the first time, species and regions that might benefit from assisted colonisation management. I find the highest proportion of AC candidate species are located in the species rich tropical regions of the Amazon, Eastern Africa and South-east Asia, but the northern Nearctic and Palearctic regions also have a high proportion of AC candidates. Dispersal ability, current range extent and the mean latitude of a species range are all significant predictors for AC candidates. Overall, I identify 1,230 species as AC candidates (by 2050), which is >10% of all global bird species. This suggests that AC may become a necessary tool for conserving species in the future and highlights the need to further investigate its potential.

5.2 Introduction

Current extinction rates are estimated to be orders of magnitude higher than background levels (Myers, 1990; Leaky & Lewin, 1992; De Vos *et al.*, 2015) and this situation is expected to worsen in future (De Vos *et al.*, 2015), with climate change predicted to be a significant driver of future extinctions (McCarty, 2001; Root *et al.*, 2003; Thomas *et al.*, 2004). A species response to climate change is likely to be dependent on its ability to track climate change (Warren *et al.*, 2001). The inability of a species to respond to climate change by altering its range due to dispersal limitations or human barriers could expose the species to serious threat (Midgley *et al.*, 2002; Broennimann *et al.*, 2006). A conservation concept that has been increasingly discussed in this context is the assisted colonization of species. Assisted colonisation (AC) is the relocation of a species beyond its natural dispersal ability, to protect it from human induced threats (Ricciardi & Simberloff, 2009b). It is needed when climate change is so rapid, that the speed at which the climate envelope shifts exceeds the dispersal ability of the species or where barriers prevent the dispersal of the species (McLachlan *et al.*, 2007; Travis *et al.*, 2013). The IUCN has officially recognized AC as a conservation tool and published guidelines for the translocations of species in 2013 (IUCN/SSC, 2013), but the first known relocations of species beyond their natural dispersal range have happened long before (Seddon *et al.*, 2015). The first documented AC was executed by Richard Treacy Henry, who moved more than 700 Kakapo and Kiwis to Resolution Island after the introduction of stouts to the New Zealand mainland (Ormerod, 1993; Seddon *et al.*, 2015).

The use of assisted colonisation (AC) as a conservation tool is controversial due to the risks associated with translocating species into novel areas beyond their native dispersal range (Mueller & Hellmann, 2008; Ricciardi & Simberloff, 2009a). It is difficult to predict the impact an introduced species can have on a community or on the wider ecosystem, and relocation can result in unanticipated damage (Mueller & Hellmann, 2008; Ricciardi & Simberloff, 2009a; Sandler, 2010). Frameworks to assess the risk of assisted colonisation and to manage the process to minimize risk have been developed (Hoegh-Guldenberg *et al.*, 2008; IUCN/SSC, 2013). Complementary tools to lower the risk at different stages throughout the process have been suggested, such as the use of multi-criteria analysis to identify recipient sites for the relocation of a species (Dade *et al.*, 2014). Furthermore methodological frameworks have been suggested, combining SDMs and population models to evaluate the necessity of relocation and to optimize recipient site selection. (Chauvenet *et al.*, 2013a). Similarly, decision framework have been proposed to help identify the ideal point in time for the relocation of a species (McDonald-Madden *et al.*, 2011).

In New Zealand, AC is already well-established as a conservation tool to remove species from the threat of introduced predators (Saunders & Norton, 2001; Seddon, 2010). With the pressure of

climate driven extinctions assisted colonisation has become more widely discussed for a variety of species (Marris, 2008). AC in the context of climate change has already taken place. The Marbled White butterfly (*Melanargia galathea*) was used as an early test-case of the potential for SDMs to identify sites for the translocation of climate-threatened species (Willis *et al.*, 2009b). An example necessitated by already-changing conditions was the translocation of seeds of the Florida Torreya (*Torreya taxifolia*) in North America (Barlow & Martin, 2004). A candidate species for assisted colonisation due to climate change should be unlikely to be capable of naturally tracking changing conditions and preferably a species that plays a minor ecological role, since dominant or keystone species are thought to be more problematic to relocate (Hunter, 2007). It is unknown how many climate-threatened species there are, that have suitable habitat beyond their dispersal ability in which they could thrive, and which might therefore be assisted colonisation candidates (Thomas, 2011). Traits that have previously been associated with species requiring AC are low dispersal ability, narrow range, low adaptation capacity and a long generation length, or being a specialist species (Loss *et al.*, 2011; Gallagher *et al.*, 2015).

Here, I identify potential candidate species that fulfil the criteria of (a) being predicted to be at serious risk from future climate change and (b) being unlikely to alter their range sufficiently quickly to track changing climate; the latter, being based on their dispersal ability. I will identify candidate species for AC amongst the terrestrial birds of the world, by identifying species that fulfil (a) and (b) and which also have suitable habitat and climate co-occurring beyond their dispersal capability. Using this approach, I summarize for the first time, species and regions that might be appropriate for assisted colonisation management.

5.3 Methods

Species distribution data

I used global breeding range polygons from BirdLife International (BirdLife International & NatureServe, 2012) for 9,196 terrestrial bird species. The species distribution polygons were gridded following the methods described in Chapter 3, using a 0.5° grid for species with a wider range (range ≥ 50 cells) and a 0.25° grid for species with a narrow range (<50 cells). Pseudo absences were selected following the distance weighted approach described in Chapter 2.

Climate data

I used the four bioclimatic variables that were selected in Chapter 2: temperature seasonality, maximum temperature of the warmest period, annual precipitation and precipitation seasonality to model species distributions. The bioclimatic variables was obtained from WorldClim and based on three different global climate models (GCMs) CCSM4, GFDL-CM3 and HadGEM2-ES, as described in Chapter 3. Future distributions are projected for the time period centred around 2050 (mean for 2041 – 2060), as well as the time period centred around 2070 (mean for 2061 – 2080). The analysis and results in this chapter are based on a medium emission scenario of future greenhouse gas emissions (rcp45).

Species distribution modelling and predictions

Projections of the current and future occurrence of species-specific climatic suitability are based on the ensemble median values of three SDMs: General Additive Models (GAM), Generalized Linear Models (GLM) and Random Forest (RF). The details for the used modelling methods are described in Chapter 3. For wide-ranging species (modelled on the 0.5° grid), predictions of climatic suitability were made to the realm the species currently occurs in and to adjoining realms in order to identify candidate areas of suitable climate that a species might conceivably reach in the future (Chapter 3, Figure 3.1). Projections of the future regions of climatic suitability for restricted-range species were based on projecting species-specific SDMs to areas of the current range extent plus a further 1000 km buffer, as described in Chapter 3.

To estimates the extent of climatically suitable areas for a species thresholds were applied to the climate suitability projections, resulting in a binary dataset to denote suitable/unsuitable areas. The threshold value used was based on maximising the kappa statistic (Cohen, 1960) across all possible thresholds, as described in Chapter3.

Habitat and dispersal data

I obtained primary habitat preferences for each species from BirdLife International (BirdLife International & NatureServe, 2012); the habitats being based on the IUCN level one habitat classifications. I used the global 'land use' data from the European Space Agency (ESA), available at a 300m resolution, and gridded the data onto a 0.5° grid to match it with the species distribution data (ESA Climate Change Initiative, 2014). I matched the IUCN level one habitat classifications with the 2010 ESA Global Land Cover data, following a crosswalk classification developed by BirdLife International and IUCN (Butchart et al. unpublished work, 2016).

Calculating potential current and future distribution

I derived areas of both suitable habitat and climate for each species by intersecting the species specific primary habitat requirements described above with the areas of suitable climate for that species (from the SDMs) within the projected area. I estimated the extent of suitable habitat within climatically suitable areas for each species for (a) the present period. I then estimated the extent of suitable climate and habitat (b) within its potential future dispersal potential and (c) beyond its dispersal potential. Estimates of the current distribution were made based on the modelled current ranges. We term this combination of a climatically suitable landscape and areas of appropriate habitat as 'climatically suitable habitat'. To estimate the dispersal potential of a species between the present and a future period (either 2050 and 2070) I used species-specific trait data (age at first breeding & natal dispersal distance) as described in Chapter 3. Using a latitude/ longitude grid instead of an equal-area grid means that cells at the equator contain more land mass than cells at very high latitudes, which could affect inference of changing range extents, especially if ranges are tending to move poleward. Consequently, to accurately estimate aerial extent I used the 'raster' package in R, to produce true areal estimates of individual grid cells (R Developement Core Team, 2012; Hijmans, 2015).

5.3.1 Identifying assisted colonisation candidates

The criteria I use to select candidate species for AC are guided by the IUCN criteria to assess species' threat categories. I selected as candidates AC species those that were projected to ≥70% reduction in range extent, based on the IUCN criteria of a ≥70% decline in population size classifying a species 'Endangered' (IUCN, 2012). From this pool of species, I then selected those species that have ≥ 20,000 km^2 of climatically suitable habitat beyond their dispersal range (equivalent to eight 0.5^o cells). This second metric of AC candidate selection aimed to identify as candidate species only those species that could be translocated in areas that could become sufficiently large to support a sustainable population. 20,000 km^2 was used as the minimum area required to advocate AC, as species occupying a range smaller in extent than this figure, and face additional threats such as

habitat fragmentation or continuing population decrease, are classified as 'Vulnerable' (IUCN, 2012). Hence, the corollary of this is that a species not facing such threats, and with a range larger than 20,000 km^2 would not be classified as vulnerable. Of course, in some situations translocating species into smaller areas of suitable habitat might be useful and necessary, which we discuss later. However, here we consider only species with a perceived high likelihood of AC success as AC candidates.

5.3.2 Predictors of AC candidate species

I used random forest (RF) models to investigate if there are attributes that make species more likely to be AC candidates. RFs do not have the same assumptions of independence as other statistical approaches (Cutler *et al.*, 2007), which avoid having to apply a phylogenetically controlled model; the avian global phylogeny remains a contentious subject (see Chapter 6). The candidate predictors of AC were the natal dispersal ability of a species, mean range latitude, current range extent, mean age at first breeding, feeding guild and the order to which a species belongs. I used cross-validation to define the two main parameters required for RF models: the number of trees (ntree) and the number of predictors used to build each tree (mtry), as described in Chapter 3. I produced ten final models, each time using a random subset of 90% of the data to fit the model and using this to predict to the 10% left-out data. I assessed model performance using AUC (Fielding & Bell, 1997). I calculated the relative variable importance, by dividing the importance of each variable by the summed importance of all variables for each model (Howard *et al.*, 2015) and produced partial dependence plots for all important predictors (Friedman, 2001). The partial dependence plots indicate the direction of a predictor's effect.

5.4 Results

5.4.1 Assisted colonisation potential candidate species

Under a medium emission scenario (rcp45) and the assumption that the habitat remains the same, 929 species are predicted to have no areas of climatically suitable habitat remaining within their dispersal capability by 2050.Of these, 758 have insufficient climatically suitable habitat beyond their dispersal capability to meet our minimum area criteria for AC candidates (>5000km^2), leaving 171 AC candidate species. 1,427 species are predicted to decline in range extent by 70-99% in future, after considering their dispersal capability. Of these, 1,059 are projected to have sufficient climatically suitable habitat beyond their dispersal capability to be considered as AC candidates. In summary, of the 9,196 species we model, 1,230 (13% of all bird species) could be considered AC candidates in the period to 2050.

By 2070, 996 species are predicted to have no climatically suitable habitat within their dispersal capability, but only 177 of these species have sufficient suitable habitat beyond their dispersal capability (>5000km^2) to be AC candidates. A further 1,615 species are predicted to decline in range extent by 70-99% in future, of which 1,205 have sufficient climatically suitable habitat (>5000km^2) beyond their natal dispersal capability and could be considered AC candidates. To summarise for the period to 2070, 1,382 could be considered AC candidate species, i.e. 15% of the global avifauna.

The species identified as AC candidates are currently classified from among all of the IUCN threat categories, but a high proportion is currently classified as “Least Concern” (Figure 5.1). Most species classified as candidates for AC by either 2050 or 2070 have an estimated total maximum dispersal of <50km throughout both time periods (Figure 5.2). The identified AC candidates come from across all feeding guilds, but the majority of them are insectivores. Frugivorous and nectarivorous species have the highest proportion of AC candidates (Figure 5.3).

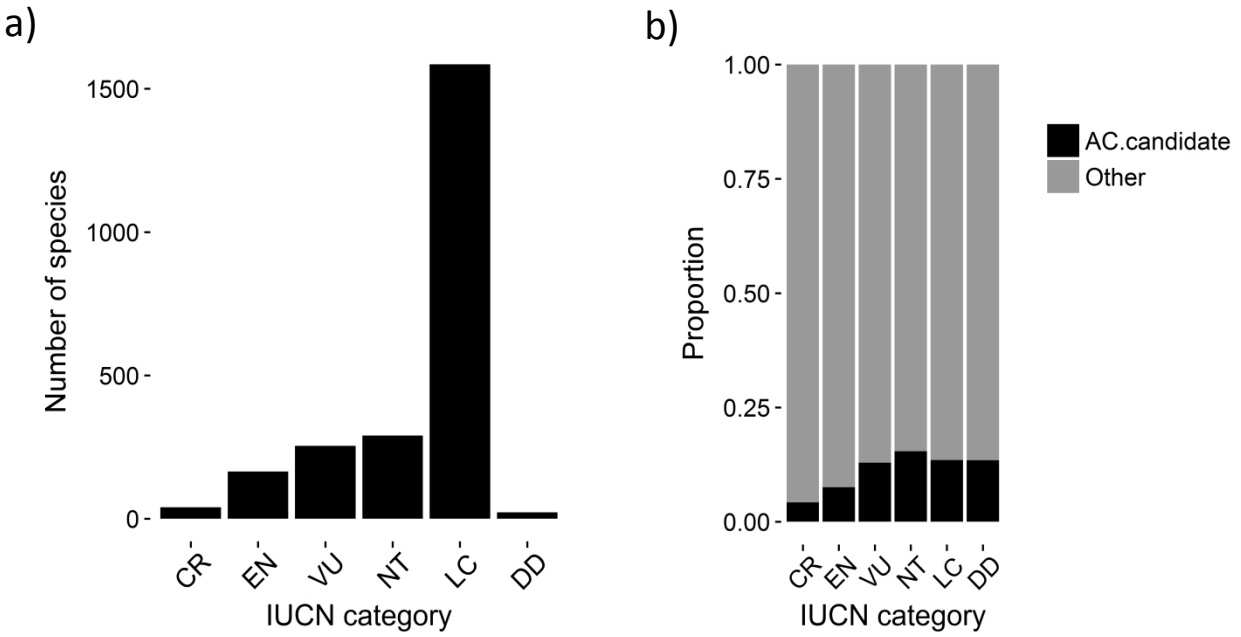


Figure 5.1: The number of species within the different IUCN threat categories that are considered AC candidates by (a) 2050 and (b) the proportion of AC candidate species across the different IUCN threat categories. (Threat categories across AC candidates by 2070, Figure S5.1)

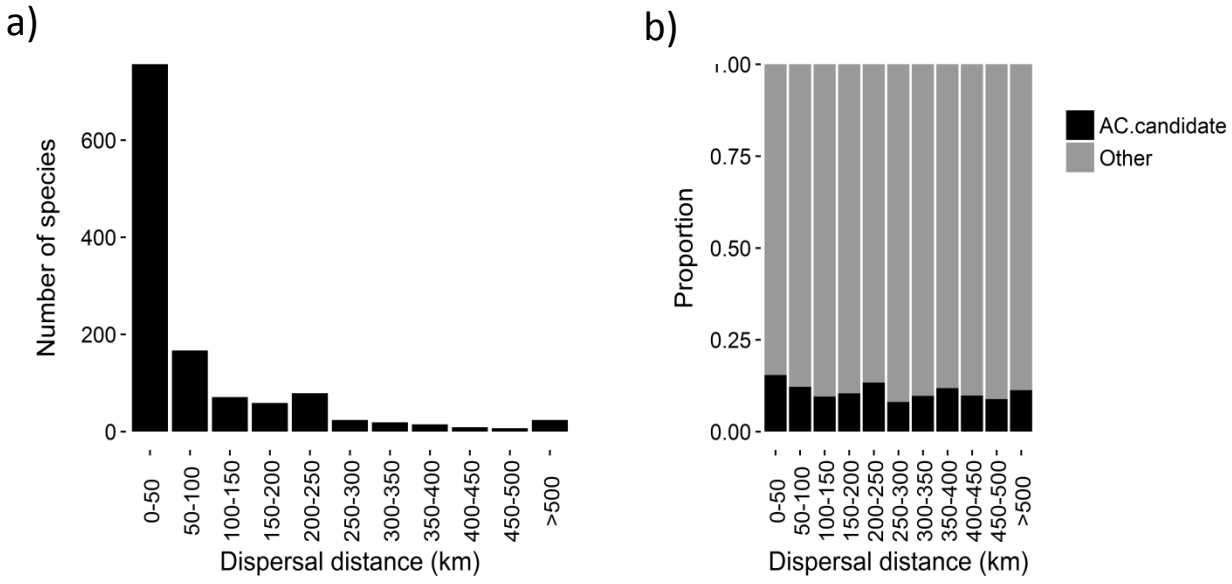


Figure 5.2: The number of species with differing dispersal capabilities that are considered AC candidates by (a) 2050 and (b) the proportion of AC candidate species across different dispersal distances. (Dispersal distances across AC candidates by 2070, Figure S5.2)

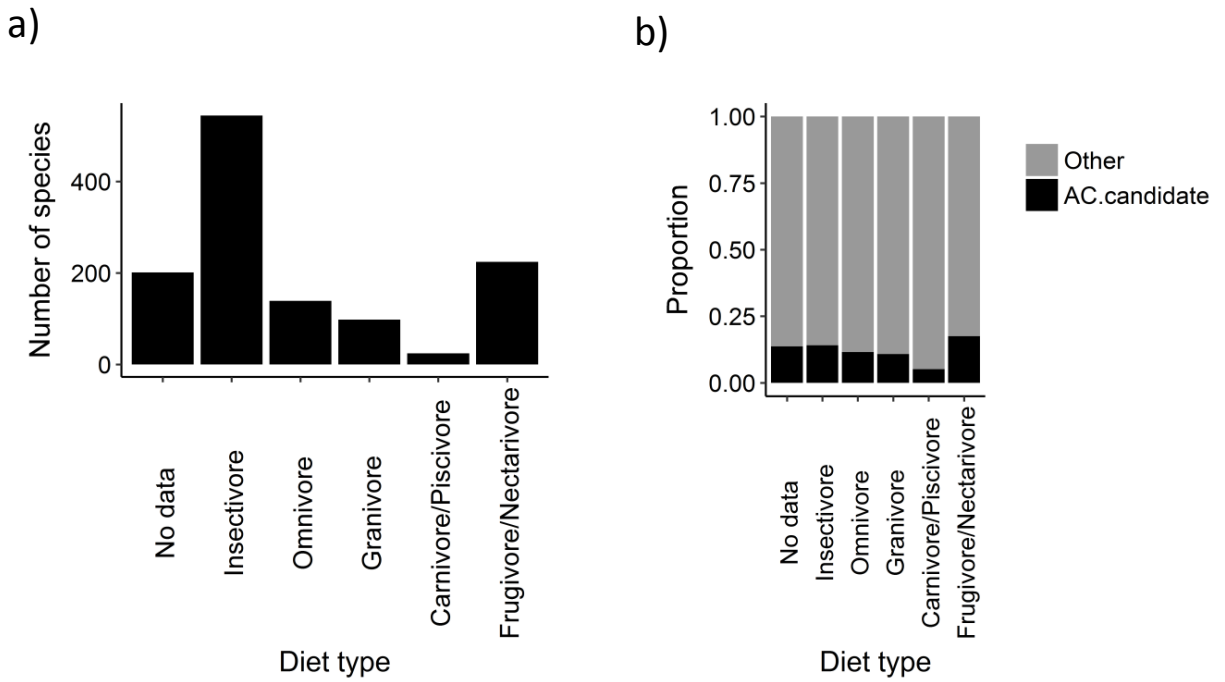


Figure 5.3: The number of species belonging to different feeding guilds that are considered AC candidates by (a) 2050 and (b) the proportion of AC candidate species across the different feeding guilds. (Feeding guilds across AC candidates by 2070, Figure S5.3)

5.4.2 Distribution of candidate AC species

Current hotspots of occurrence of AC candidates are located mainly in the Amazon basin and the Andes, but also East Africa, the Himalayas and some of the islands in South East Asia, mainly the Philippines and Sulawesi, have higher numbers of potential candidates (Figure 5.4). Calculating the proportion of AC candidate species within each grid cell, confirms the observed pattern of AC candidate hotspots being located across the species rich tropical areas of the world but shows that the northern Palearctic and Nearctic also have a high proportion of AC candidates (Figure S5.4).

Localities of climatically suitable habitat for translocating AC candidates show some clear patterns (Figure 5.5), for example, in the Amazon basin and the Andes. Candidate AC cells that have the potential to host numerous AC candidates in this region are to the north of the current range boundaries of the candidate species, i.e. along the northern edge of South America, into Central America and along the Andes. In East Africa, the patterns are less clear and cells with suitable habitat and climate space for the selected species are more spread out. The cells suitable for the highest number of assisted colonisation candidates here are located in the Albertine Rift Valley. The pattern in South East Asia is similar with no distinct hotspots, with cells having suitable habitat and climate space being located on Borneo and Sumatra.

The observed pattern in the distribution of potential candidates for assisted colonisation by 2070 is very similar. Hotspots for the current distribution of potential candidates are the Amazon basin, the Andes, Eastern Africa, the Himalayas and South East Asia, especially the Philippines and Sulawesi (Figure 5.6). The suitable habitat and climate space beyond the natural dispersal range of these species lies north of the current range boundaries or in the Andes in South America, north of the range boundaries for potential candidates in Eastern Africa and mainly on Borneo and Sumatra in South East Asia (Figure 5.7).

Plotting the projected current and future suitable habitat and climate space of different selected AC candidates, shows that there are different patterns that lead to a candidate species being flagged up. Figure 5.8 (a to c) displays a species whose suitable habitat and climate space is projected to disappear on the island it is currently inhabiting. Figure 5.8 (d to f) displays a species whose suitable climate envelope moves faster than the species is able to disperse (modelled dispersal ability for *Hylopezus berlepschi* ~ 0.06km per year, Joe Tobias unpublished data).

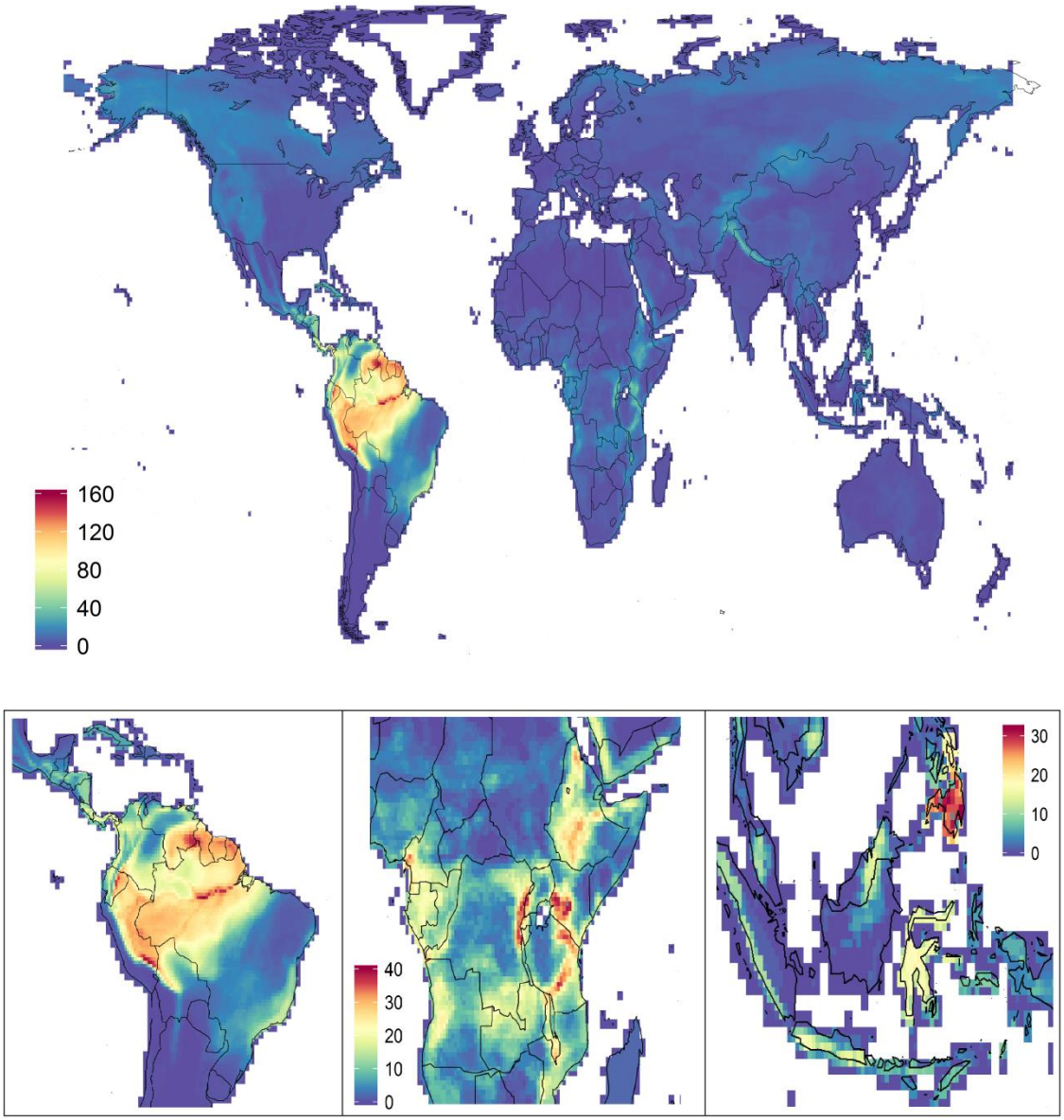


Figure 5.4: Current richness of the 1,230 AC candidates by 2050, based on the rcp45 emission scenario. Plots are based on ensemble median projections from the three SDMs and richness values plotted are means across three GCMs. Note plots for Africa and South East Asia are rescaled.

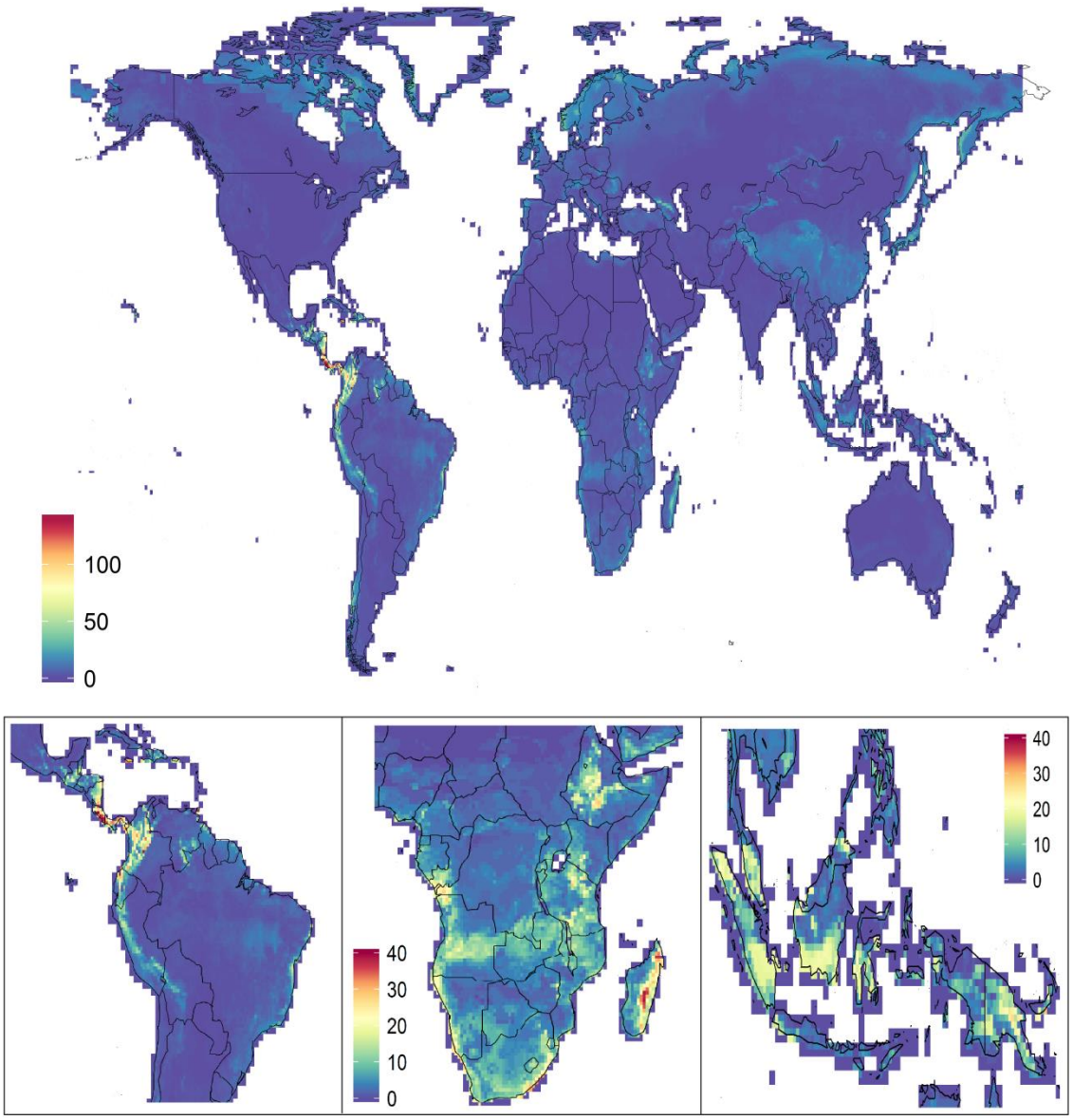


Figure 5.5: Potential future richness of the 1,230 AC candidates at sites beyond their dispersal capabilities by 2050, i.e. the plots overlay the AC sites for all AC candidate species. Distributions are based on ensemble median projections from the three SDMs and richness values plotted are means across three GCMs. Note plots for Africa and South East Asia are rescaled.

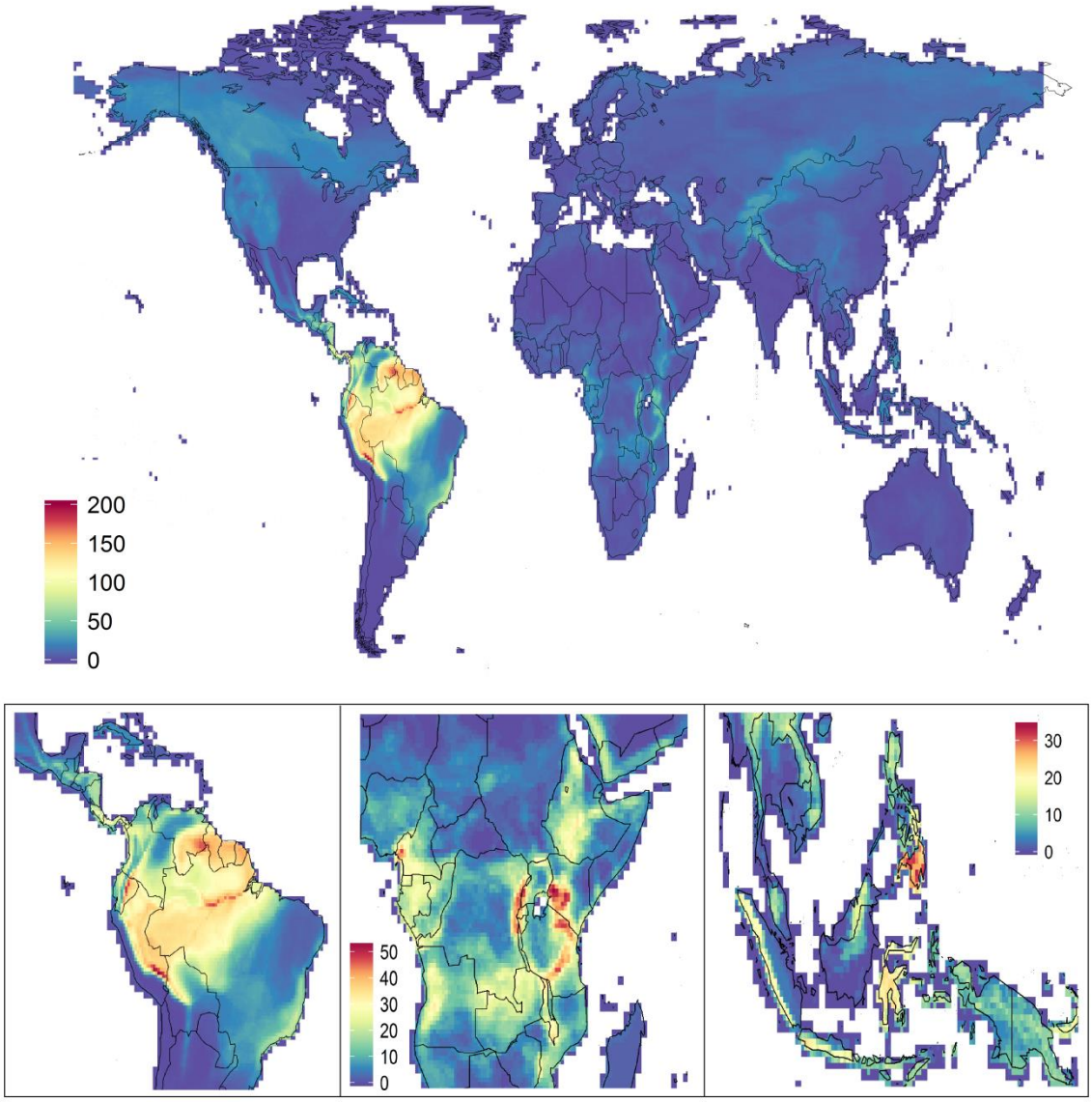


Figure 5.6: Current richness of the 1,382AC candidates by 2070, based on the rcp45 emission scenario. Plots are based on ensemble median projections from the three SDMs and richness values plotted are means across three GCMs. Note plots for Africa and South East Asia are rescaled.

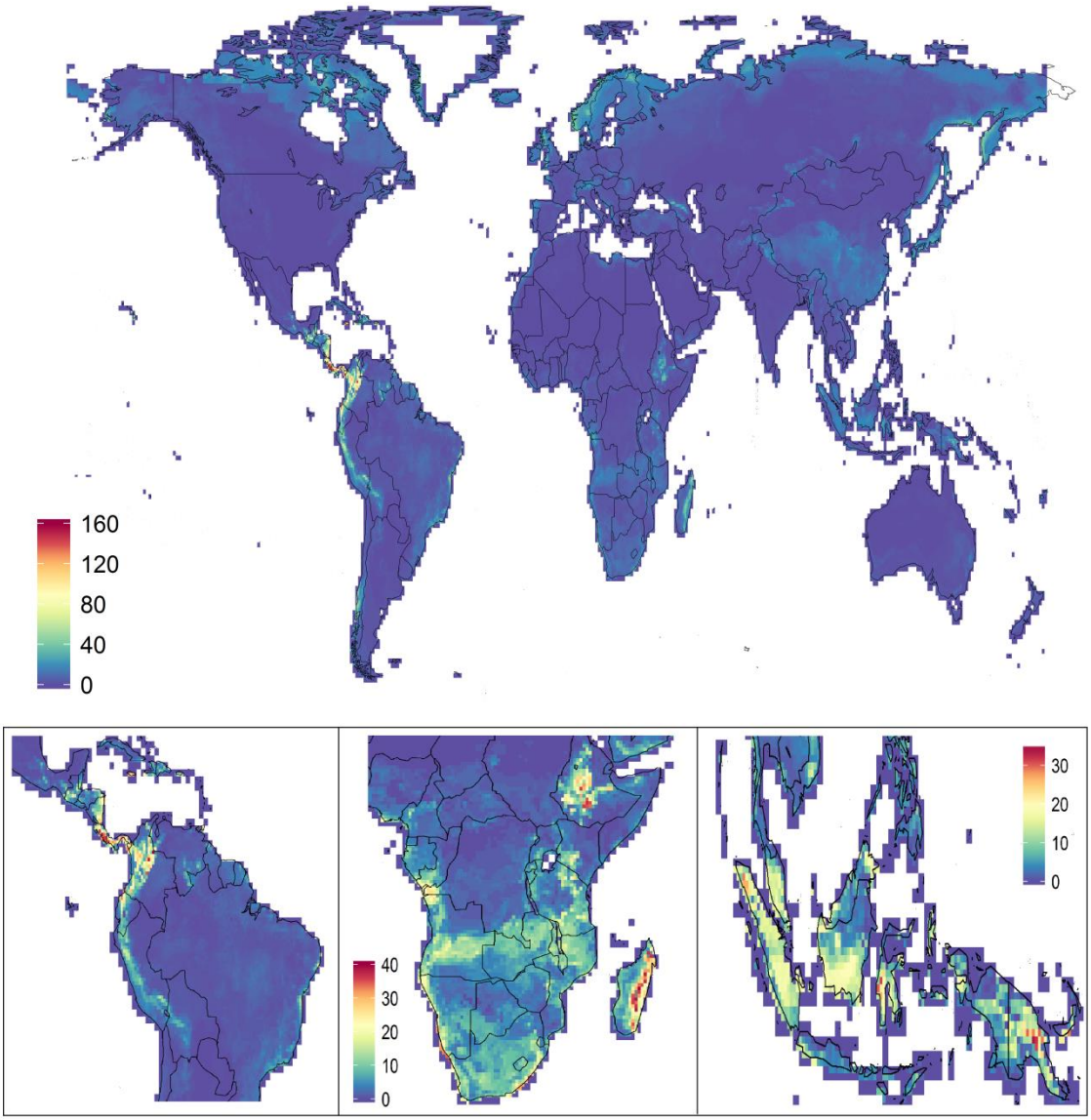


Figure 5.7: Potential future richness of the 1,382 AC candidates at sites beyond their dispersal capabilities by 2070, i.e. the plots overlay the AC sites for all AC candidate species. Distributions are based on ensemble median projections from the three SDMs and richness values plotted are means across three GCMs. Note plots for Africa and South East Asia are rescaled.

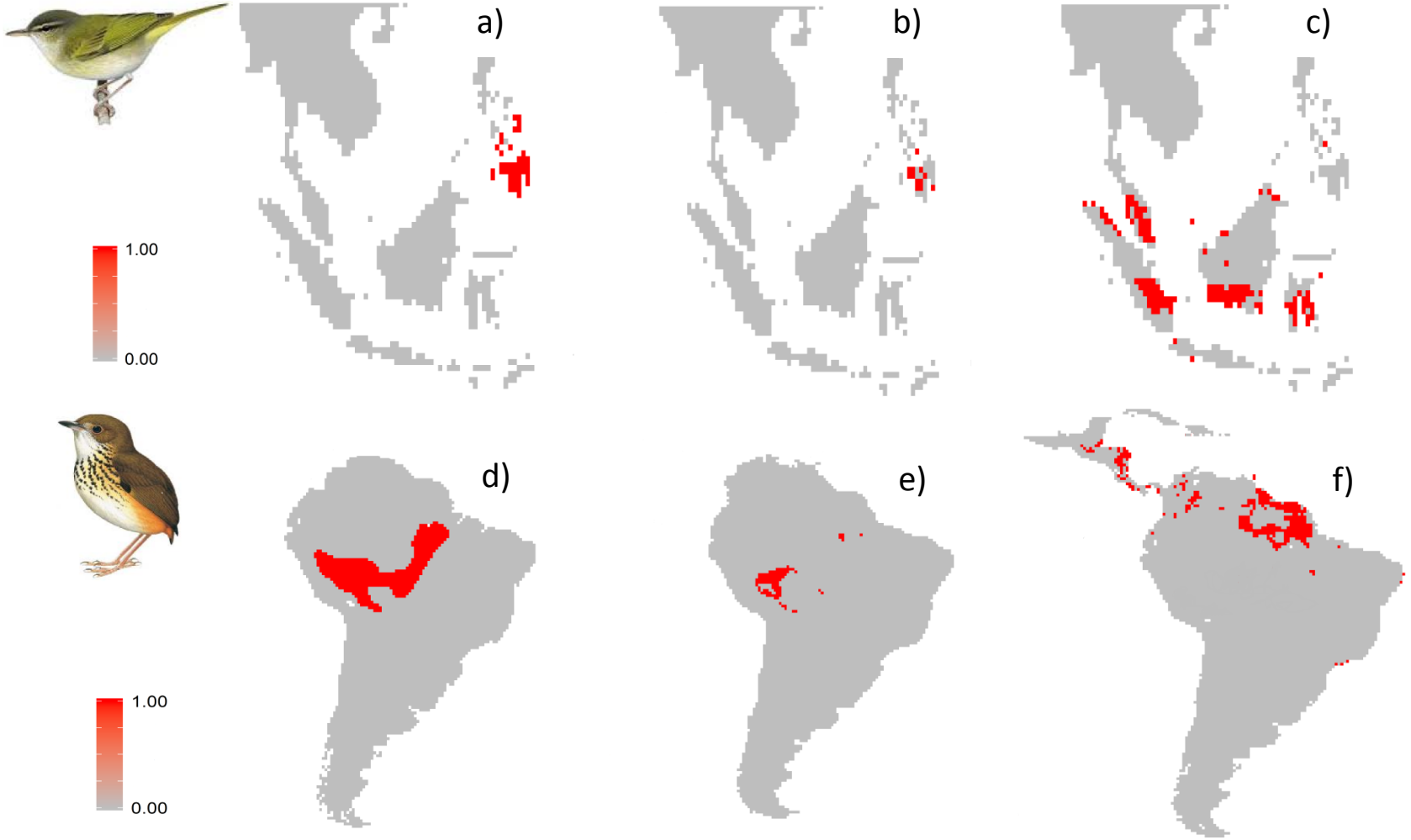


Figure 5.8: Example species selected as AC candidates. Projected suitable habitat and climate space of *Phylloscopus olivaceus* (a,b,c) and *Hylopezus berlepschi* (d,e,f), Distributions shown for (a,d) the present and (b,e) projected for 2050 , along with (c,f) climatically suitable habitat beyond the species' dispersal ability by 2050. *Hylopezus berlepschi* is an example for a species being unable to keep up with the velocity of climate change, *Phylloscopus olivaceus* is an example for a species being prevented from keeping up by a dispersal barrier (open water) (Species pictures, © Handbook of the Birds of the World, fair dealing).

5.4.3 Predictors of AC candidate species

The relative variable importance of the different predictors indicated a species' current range extent, dispersal ability, and mean range latitude are the strongest predictors of AC need. The predictors varied significantly in their importance (Figure 5.9, ANOVA, $F_{(6/620)}$ =2821, $p < 0.0001$). A post hoc Tukey test showed that the variable importance between all predictors was significantly different ($p < 0.0001$), besides IUCN category and Mean age at first breeding which were not different from each other in their importance ($p = 0.71$).

The partial dependence plots show that, a narrow range extent (Figure5.10a), tropical or high northern range latitudes (Figure 5.10c)) and very low or high dispersal ability are positive predictors for AC candidates (Figure 5.10b).

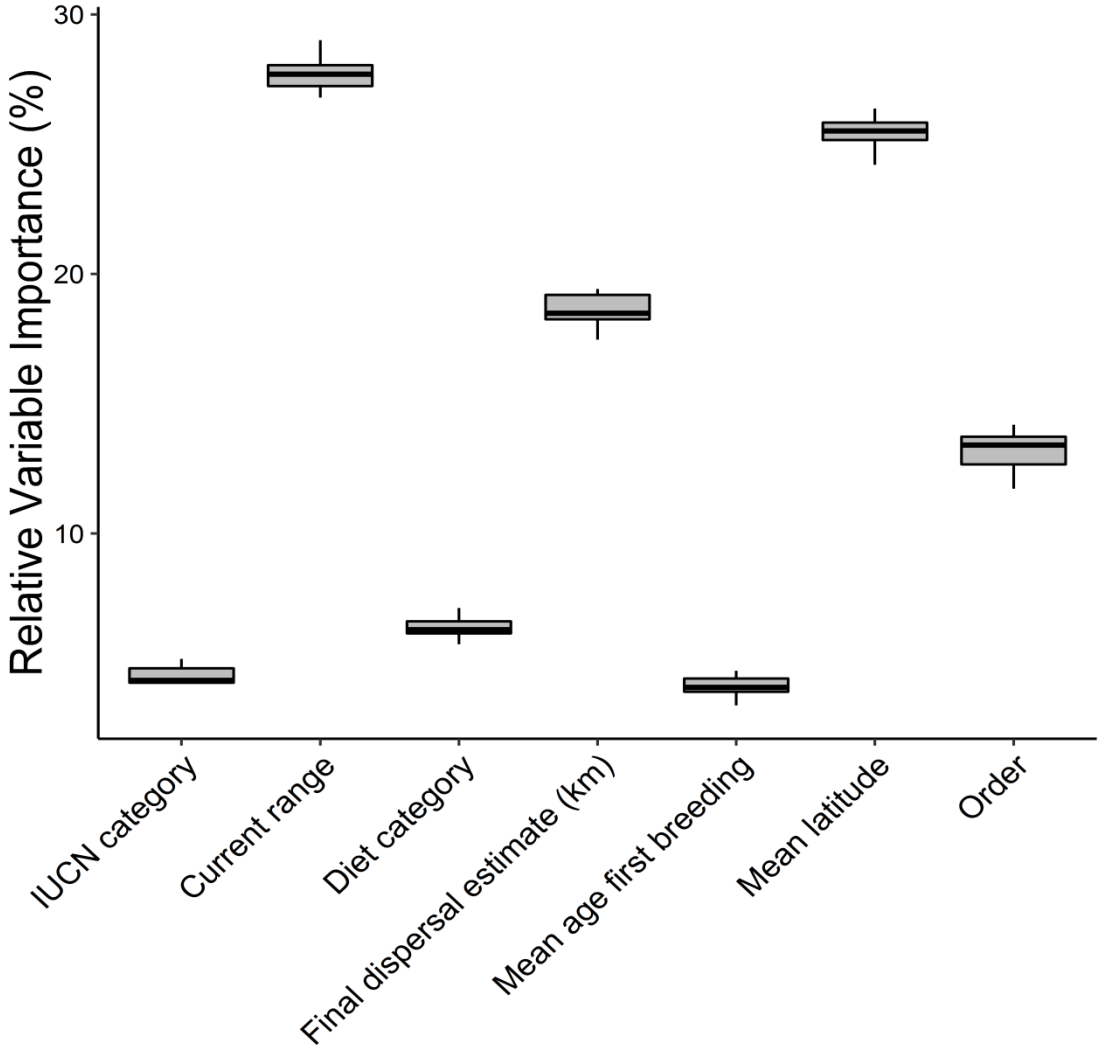


Figure 5.9: Random forest relative variable importance of species attributes to determine AC candidate species.

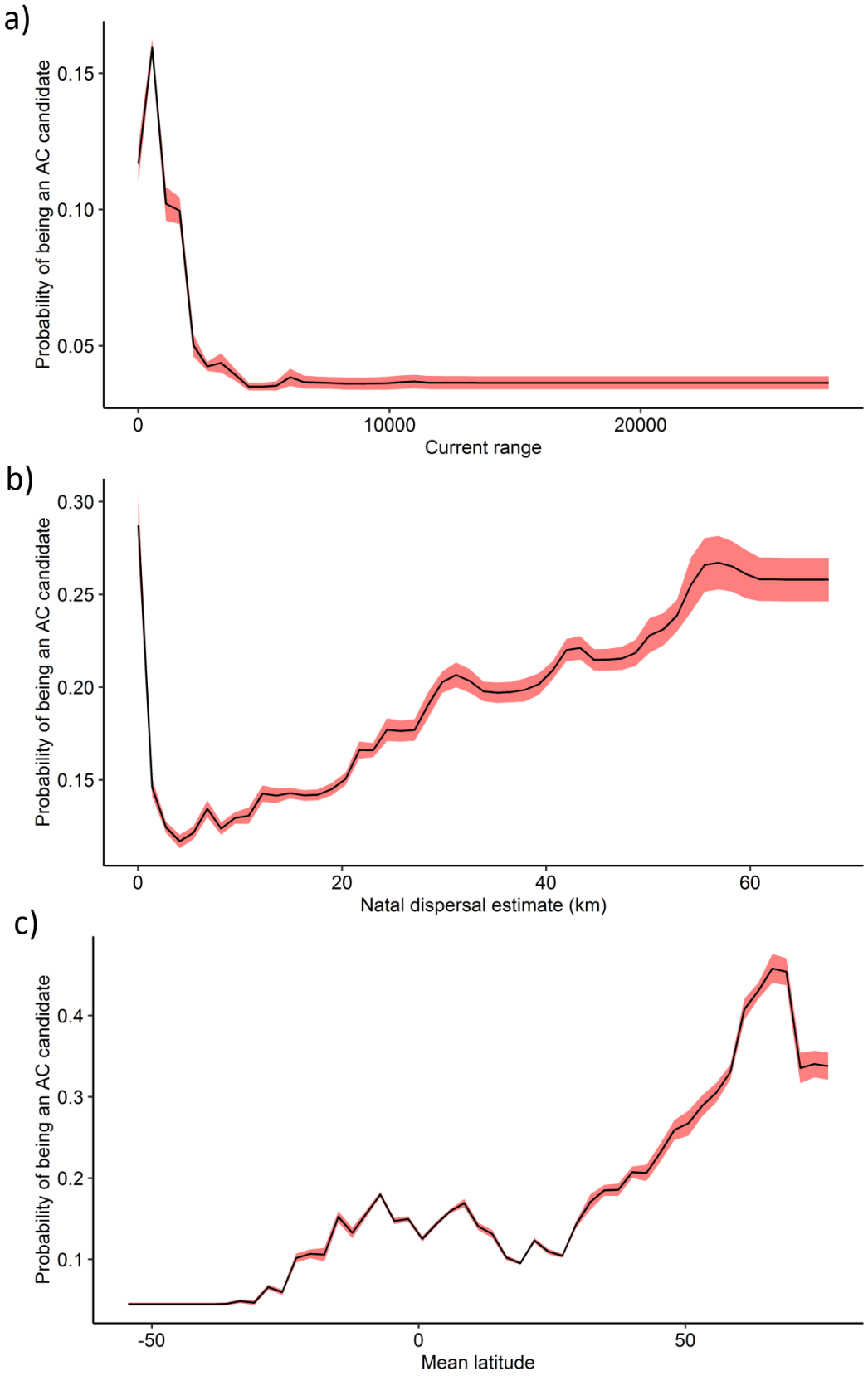


Figure 5.10: Partial dependence plots from the random forest models for the three most important variables (a) Current range extent, (b) Natal dispersal ability in (km), (c) Mean latitude a species occurs at.

5.5 Discussion

About one quarter of the modelled species are predicted to decline in range extent by ≥70% by 2050 without intervention. Of these species, nearly 60% are projected to have climatically suitable habitat (>5000km^2) beyond their dispersal capability. Figures are similar when considering the period between now and 2070; by the end of this period 28% percent of modelled species are predicted to decline in range extent by ≥70% and 68% of these are projected to have climatically suitable habitat beyond their dispersal capability. The majority of these species are located in the species-rich tropical regions of the Amazon, East Africa and South-east Asia. Displaying the numbers of AC candidates, as the proportion of species (Figure S5.4) in a grid cell, shows that this is not solely an artefact of the high species richness but that the Amazon still harbours a high proportion of AC candidates. The other tropical regions stand out less when considering the proportion of AC candidates in a cell, instead the norther Palearctic and Nearctic show to have a considerably high proportion of AC candidates.

The projected changes might not be realised by 2050 at to the predicted extent and could be hard to detect initially. Changes in vegetation might lag behind climatic changes (Davis, 1989; Bertrand *et al.*, 2011), leading to a delayed response of avian communities. Even if habitat changes occur rapidly, birds may still have a delayed due to dispersal limitations, leading to an 'extinction debt' (MacArthur, 1967; Hanski & Ovaskainen, 2002; Kuussaari *et al.*, 2009). Delayed responses of species to recent climate change have already been documented (Menéndez *et al.*, 2006). Delayed species responses can make it difficult to validate the models that project long-term changes. Monitoring of the areas and species identified here as being projected to change in richness and range will be necessary to evaluate the extent and rate at which projected changes eventuate.

The important predictors of AC candidates were the current range extent of a species, the dispersal ability and the latitude of a species range centre. These predictors conform to previous suggested traits of AC candidate species. Gallagher *et al.* (2015) identified nine traits which make a species a likely candidate, amongst which were the dispersal ability of a species and a narrow distribution. The partial dependence plots highlight that the significant predictors act in the expected manner. For example, a narrow current range extent and low dispersal ability increase the probability of a species being identified as an AC candidate.

AC is a non-trivial conservation intervention that may be inappropriate in many cases. Hence, many of these species might turn out not to be suitable candidates for AC. Each case would need to be considered individually and evaluated for its suitability based on its biology, the availability of a recipient community, the costs and the estimated risk associated with each case (Hunter, 2007;

Hoegh-Guldenberg *et al.*, 2008; Rout *et al.*, 2013). Guidelines for the vigorous assessment of AC candidates and recipient sites have been suggested and applied during early case studies (Chauvenet *et al.*, 2013b; Rout *et al.*, 2013), to maximise the potential success of an AC. Additionally, to evaluate whether AC will benefit a species, whilst avoiding a negative impact on the recipient community, the value of the species and any ethical problems should also be considered on a case-by-case basis (Sandler, 2010). The high numbers of species that are threatened by climate change but that appear to have a substantial amount of climatically suitable habitat beyond their natural reach emphasizes the import role AC could play in future species conservation to mitigate climate change impacts. Here we used a coarse metric of suitable habitat, based on a 0.5° grid and counting a cell as suitable if it contains the primary habitat of a species to any extent. Further assessments of more finely resolved, and detailed, habitat requirements for individual species will be needed to identify if the habitat beyond a species dispersal range is truly suitable. Here, I provided a long-list of candidate species that would be suitable for further investigation.

AC has sparked heated debates amongst conservationists. The attitude towards AC, which puts different conservation goals at odds with each other (McLachlan *et al.*, 2007), often depends on the field of study. Researchers working in continuous ecosystems, which have few dispersal limitations, or those working on rare, narrow-ranging endemics are more likely to contemplate the idea of relocating a species beyond its natural dispersal ability (McLachlan *et al.*, 2007; Vitt *et al.*). Researchers working in the field of invasions are, on the contrary, more likely to be opposed to AC (McLachlan *et al.*, 2007). Opinions range from AC being a pragmatic and cost effective conservation tool (Hunter, 2007; Hoegh-Guldenberg *et al.*, 2008) to describing it as 'ecological gambling', due to the possibility that the species which is being transferred to be saved from extinction could in the worst case lead to the extinction of other species (Ricciardi & Simberloff, 2009a). There are a variety of risks associated with the introduction of a species outside its natural range. In particular, the danger of an introduced species becoming invasive which could have severe consequences for the recipient community and whose impacts and long term ecological costs are not yet fully understood (Strayer *et al.*, 2006; Ricciardi & Simberloff, 2009a; Ricciardi *et al.*, 2013). Invasive species can cause disruptions in the food web, the extirpation of local species, and the loss of ecosystem services (Spencer *et al.*, 1991; Dick *et al.*, 2013; Walsh *et al.*, 2016; Mollot *et al.*, 2017). Predicting if a species considered for translocation will become invasive is especially difficult since the traits that cause species to become endangered are not necessarily the opposite of those that cause species to become invasive (Kolar & Lodge, 2001; Jeschke & Strayer, 2008a; Ricciardi & Simberloff, 2009a).

Nevertheless, there are different approaches to AC, each of which carries a differing amount of risk. Generally, translocating a dominant or keystone species is thought to involve greater risk (Lunt *et al.*, 2013). Many of the previously introduced species that have turned into problematic invasive species, and caused serious disruption to their recipient communities, were translocations from mainland to island ecosystems, and problematic invasives have more frequently arisen from intercontinental and long distance introductions (Hoegh-Guldenberg *et al.*, 2008; Thomas, 2011). One type of AC that carries relatively lower risk is the short-distance AC of species that might have dispersed to novel areas naturally but are in habitats that have been severely fragmented by human activity, and which are therefore now unable to move through the landscape unaided (Hoegh-Guldenberg *et al.*, 2008; Vitt *et al.*; Wilson *et al.*, 2009). In those cases, AC might be more cost efficient than for, example, the construction of stepping stone sites or corridors traversing the novel barrier (Willis *et al.*, 2009b). Another approach to help limit species declines due to climatic change that doesn't involve translocating the species beyond its natural dispersal range, is to translocate more heat tolerant individuals of a species to historically colder areas within the species range (Berkelmans & van Oppen, 2006; Hoegh-Guldenberg *et al.*, 2008). The rationale behind this is to support the thermal adaptation of species by moving individuals with a high thermal tolerance, from populations at the lower latitude boundaries of a species range, to populations located at the higher latitudes of its range boundaries. Local thermal adaptation has been found across a variety of species e.g. in corals, butterflies, fruit flies and frogs (Balanyá *et al.*, 2006; Berkelmans & van Oppen, 2006; Kingsolver *et al.*, 2007; Phillimore *et al.*, 2010).

AC is usually discussed in the context of saving endangered species by translocating them to keep pace with their climatic niche, in cases where species are unable to naturally alter their range rapidly enough, or where they are hindered from dispersing by habitat fragmentation or other human barriers. However, AC could also, in some situations, benefit the recipient communities. Potential benefits range from the restoration of ecological functions, by introducing species with similar properties to lost keystone species, consequently recreated communities dynamics that have been lost for thousands of years (Donlan, 2005; Lunt *et al.*, 2013). For example, it has been suggested that the introduction of African cheetah, elephant and lion to USA could restore ecological function that has been lost since the eradication of native US species that performed similar functions (Donlan, 2005). However, such arguments tend more into the realms of rewilding and ecological function restoration, rather than considering rewilding to prevent species loss and extinction of the translocated species, which is the focus on AC here, in the context of climate change.

The translocation of a threatened species solely for the purposes of conserving the translocated species usually has only limited benefits for the recipient community (Lunt *et al.*, 2013), although they can provide additional ecosystem service value. For example, the AC of Marbled White butterflies into a novel area of northern England resulted in increased visitation of the recipient site by people seeking a locally novel species, hence increasing the cultural value of the site (S.Willis pers. comm.). Introducing a species into a community in which it could fill a vacant niche left by an extinct native could help to restore ecological function and subsequently increase the conservation impact of an assisted colonisation (Seddon, 2010; Lunt *et al.*, 2013), but this strategy is inevitably risky since it involves moving ecologically dominant or keystone species (Seddon, 2010; Lunt *et al.*, 2013). In any case, each species will require independent consideration to identify the most appropriate strategy.

The vast majority of the AC candidates identified here are projected to shift their ranges by <50 km by 2050. This figure does assume mean natal dispersal distances over the intervening period is indicative of typical range-shifting dispersal (Figure 5.2). This may not be the case for species that undertake irruptive dispersal when relocating to new areas, or for species whose natal (or inter-annual) dispersal has a long tail. Despite these caveats, the dispersal data we used here to limit potential responses to climate change are the best data currently available for most of the world's birds, and undoubtedly provides greater insight into species that are likely most threatened compared to alternative scenarios of unlimited or no dispersal. Unpublished work by S.G.Willis on new avian colonists to the UK provides some evidence that range extensions are much better projected by a combination of changing climatic suitability and the estimated colonisation period to reach a cell, where colonisation period, P, is derived as:

$$\mathrm{P} = \frac{(\text{Distance of nearest population} * \text{generation length})}{\text{mean natal dispersal}}$$

This colonisation period, which is equivalent to the dispersal estimate used here, was a highly significant predictor of actual colonisation of the UK, by those species for which it was projected (Huntley *et al.*, 2006) that the climate would become suitable during the current century (n=44 potential colonists; logistic regression of actual colonisation versus P: Z = 3.114, p=0.0018, i.e. P was a highly significant predictor of colonisation). Other studies have also suggested that species with limited dispersal ability might be especially threatened by climate change (Jetz *et al.*, 2007; Ohlemüller *et al.*, 2008).

Most of the AC candidate species I identify are currently classified by the IUCN as of "Least Concern" (Figure 5.1), indicating that climate change might threaten a different subset of species compared to

those that are currently threatened; the latter most frequently being threatened as a result of habitat loss, land-use change, hunting and invasive species (Pimm, 2008; Sekercioglu *et al.*, 2008). Candidate translocation areas for AC candidates broadly mirror the findings of previous studies that montane species in particular are especially under threat from climate change (Williams *et al.*, 2003; Raxworthy *et al.*, 2008; La Sorte & Jetz, 2010), with many of the suitable cells being located in the Andes and the Himalayas.

The identified AC candidate species come from across different feeding guilds but the highest proportion of AC candidates was in the frugivorous or nectarivorous guilds, suggesting that specialist species might indeed be more likely to benefit from AC as a conservation tool than other species (Gallagher *et al.*, 2015). This is in line with the overall higher risk of specialised species to be vulnerable to climate change (Williams *et al.*, 2008; Foden *et al.*, 2013).

There are several possibilities why a species might be unable to track their suitable habitat and climate space. The two example species shown in Figure 3.8, illustrate two commonly found patterns throughout this study, the inability of a species to track suitable climate based on very limited dispersal ability (Figure 5.8 d to f) and the inability to track suitable climate because of natural barriers (Figure 5.8 a to c). Barriers could also be caused by human modified habitat that disables the species from crossing. The latter two are good examples of the ethical challenges AC still poses. Creating corridors and stepping stones will enable a species to cross human disturbed landscape, possibly even beyond their current natural range and is usually not opposed as a conservation strategy, whereas translocation the species possibly to the same location it would reach through stepping stones is much more questioned, especially if its beyond that natural dispersal range (Lawler & Olden, 2011). It is difficult to say where the line should be drawn and case by case decisions will be needed.

Suitable areas for species, both now and in the future are based on a combination of climate suitability and the current distribution of a species' preferred habitats. This could result in the inaccurate estimation of suitable habitat in both periods if the landcover data used lack sufficient detail to describe the more refined habitat preferences of a species. For example, in the context of many tropical forest species, a more refined forest layer that separates primary forest from regrowth would potentially improve projections for many specialised forest species that depend upon primary forest. Moreover, at present the simulations of AC translocation areas, and hence of AC candidate species rely on current habitat remaining unaltered until 2050. Although this may be an acceptable assumption in the short to mid-term, it will become increasingly unlikely further into the future, hence our focus on short term AC candidates in much of this chapter. As the current

habitat layer does not reflect any land-cover changes to 2050/2070, the estimated range losses I predict could be substantially greater in future than predicted here, especially for forest species of tropical regions with high current and forecast deforestation rates (Miettinen *et al.*, 2011; Achard *et al.*, 2014). The same could also be true for other species occurring in areas with high projected land use change (Sala *et al.*, 2000; de Chazal & Rounsevell, 2009). Projections of future climatically suitable habitat might be improved by the incorporation of future projected land-use (from, for example, dynamic global vegetation models [DGVMs] and socio-economic models of change) however, these projections of changing land-use may be no more precise than assumptions of short-term habitat stasis. Incorporating future land-use projections into our AC modelling was not possible; due to the relatively recent availability of land-use projections from the latest IPCC scenarios but this work is an urgent priority that will follow on from the work presented here.

The predicted substantial declines in about one quarter of all species highlights the threat climate change poses for the world's terrestrial birds. The high number of species (13% of all the world's terrestrial birds) that have considerable amount of suitable habitat and climate space beyond their natal dispersal ability emphasises the importance AC could have as a conservation tool. Assisted colonisation is a controversial conservation strategy, but with the imminent threat of climate change it needs to be considered (McLachlan *et al.*, 2007; Sax *et al.*, 2009) even if it turns out to be not feasible in cases. When trying to preserve biodiversity under climate change, there are risks to both action and inaction (Schwartz *et al.*, 2006; Schlaepfer *et al.*, 2009).In this chapter, I highlight regions of the worlds where species are projected to experience serious range losses, the next step to further the selection of AC candidates would be to select key monitoring areas, to detect whether the projected declines can be confirmed. If declines are confirmed, highlighted key species in these areas should be selected for rigorous assessment of their suitability as AC candidates, and their potential threat to putative recipient sites evaluated (Chauvenet *et al.*, 2013b). Birds are often used as indicator species, since they have been shown to react to changes on a variety of scales, and their occurrence and abundance (Carignan & Villard, 2002). However, due to their mobility, they might differ from other taxa in their ability to track suitable habitat and climate space. Reptiles, for example, have been projected to decline globally under climate change, with Mexico being a hotspot for these projected declines (Sinervo *et al.*, 2010). By contrast, Mexico is not particularly prominent in terms of regions that have high numbers of avian AC candidates. The method used in this chapter could help to identify hotspots and candidates for assisted colonisation amongst other taxa but the hotspots of avian AC candidates are unlikely to be similar for AC candidates in other taxa.

Chapter 6

Global patterns in the divergence between phylogenetic diversity and species richness in terrestrial birds

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6.1 Abstract

The conservation value of sites is often based on species richness (SR). However, metrics of phylogenetic diversity (PD) reflect a community's evolutionary potential and reveal the potential for additional conservation value above that based purely on SR. Although PD is typically correlated with SR, localized differences in this relationship have been found in different taxa. Here, I explore geographic variation in global avian PD. I identify where PD is higher or lower than expected (from SR) and explore correlates of those differences, to find communities with high irreplaceability, in terms of the uniqueness of evolutionary histories. Here I use comprehensive avian phylogenies and global distribution data for all extant birds, I calculated SR and Faith's PD, a widely applied measure of community PD, across the terrestrial world. I modelled the relationship between avian PD for terrestrial birds and its potential environmental correlates. Analyses were conducted at a global scale and also for individual biogeographic realms. Potential explanatory variables of PD included SR, long-term climate stability, climatic diversity (using altitudinal range as a proxy), habitat diversity and proximity to neighbouring realms. I identified areas of high and low relative PD (rPD; PD relative to that expected given SR). Areas of high rPD were associated with deserts and islands, whilst areas of low rPD were associated with historical glaciation. Our results suggest that rPD is correlated with different environmental variables in different parts of the world. There is geographic variation in avian rPD, much of which can be explained by putative drivers. However, the importance of these drivers shows pronounced regional variation. Moreover, the variation in avian rPD differs substantially from patterns found for mammals and amphibians. The results suggest that PD adds additional insights about the irreplaceability of communities to conventional metrics of biodiversity based on SR, and could be usefully included in assessments of site valuation and prioritisation.

6.2 Introduction

Rapid losses of biodiversity have occurred across the globe over recent decades, driven primarily by human modification of the environment and increasing demand for natural resources (Vitousek *et al.*, 1997; Butchart *et al.*, 2010; Cardinale *et al.*, 2012). Estimates of the current rate of species extinctions are 1000 to 10,000 times higher than background levels, and this is consistent with previous mass extinction events (Leaky & Lewin, 1992; Mace *et al.*, 2000; Barnosky *et al.*, 2011). The loss of biodiversity is likely to have profound effects on ecosystem functioning (Loreau *et al.*, 2001), reducing the intrinsic resilience of these systems to environmental change (Peterson *et al.*, 1998; Chapin III *et al.*, 2000), and affecting ecosystem processes and the provision of ecosystem services (Tilman *et al.*, 2006; Worm *et al.*, 2006). Consequently, preventing the loss of biodiversity is a global priority (Rands *et al.*, 2010).

Conservation efforts *in situ* usually focus on the preservation of species and, consequently, species richness (SR) is frequently used as the metric of biodiversity for assessing spatial conservation priorities (Gaston, 1996; Gotelli & Colwell, 2001; Fuller *et al.*, 2010). SR, however, is driven largely by common and widespread species, and thus, conservation prioritisations based on this metric will often fail to capture the features of biodiversity that require the greatest conservation focus (Brooks *et al.*, 2006). To address this concern, metrics have been developed that quantify various aspects of species' irreplaceability; such metrics include the number of endemic species or the taxonomic uniqueness of species in a community (Brooks et al. 2006). These metrics aim to better account for the conservation value of individual species based on rarity or their unique evolutionary history (May, 1990; Vane-Wright *et al.*, 1991). While irreplaceability metrics have theoretical appeal, it has often proven difficult to quantify these metrics, in large part due to limitations with data, including incomplete species inventories and lack of robust phylogenies. However, for many of the major taxonomic groups (e.g. birds, mammals), distribution and phylogenetic data have become more widely available, leading to irreplaceability metrics being estimated and used more readily in conservation prioritisations (Heard & Mooers, 2000; Purvis *et al.*, 2000a; Isaac *et al.*, 2007).

Phylogenetic diversity (PD) is a measure of the evolutionary relationship between species (Hardy & Senterre, 2007) and provides a metric of biodiversity that accounts for evolutionary distances between co-occurring species (Crozier, 1997). Thus, PD can be used to quantify the taxonomic uniqueness of species in a community and to assess irreplaceability in terms of evolutionary history, functional diversity (Flynn *et al.*, 2011) and evolutionary potential (Faith, 1992; Forest *et al.*, 2007). Such irreplaceability metrics might add value over SR metrics when considered in conservation strategies (Isaac *et al.*, 2007; Isaac *et al.*, 2012). Under the assumption that closely related species have a similar evolutionary potential, but more distantly related species differ more in their

potential, a community with high PD has a higher chance of containing a subset of species with greater evolutionary potential (Winter *et al.*, 2012). Therefore, a community with high PD might be considered to have a greater potential to be robust to future environmental changes (Faith, 1992). Patterns of SR and PD tend to be highly correlated across broad spatial scales and earlier studies suggest that SR is, in general, an adequate surrogate for PD (Rodrigues *et al.*, 2005). Yet localised differences between SR and PD, as well as related measures such as phylogenetic endemism and functional diversity, have been found across a range of taxa (Davies *et al.*, 2008; Davies & Buckley, 2011; Fritz & Rahbek, 2012). A global study of amphibians found mismatches between SR and PD, with lower PD than expected (given SR) on remote islands and archipelagos, as well as in regions that have been long isolated, such as Madagascar and Australia (Fritz & Rahbek, 2012). For mammals, lower than expected PD has been identified for some mountain ranges and remote islands, whereas higher than expected PD was found in Sub-Saharan Africa and parts of the Indian sub-continent (Davies & Buckley, 2011).

Observed localized differences between SR and PD could occur for various reasons. Unlike SR patterns, which have been a central topic throughout the history of ecology (Wallace, 1878; Stevens, 1989; Palmer, 1994), exploring patterns of PD has become possible only very recently, due to the availability of comprehensive phylogenies (Cavender-Bares *et al.*, 2009; Roquet *et al.*, 2013). Consequently, the drivers of these PD patterns remain largely unknown. Important historical processes (Losos & Glor, 2003), as well as macro-ecological changes such as mass migrations (e.g. Great American Biotic Interchange; Webb 2006) and extinctions, can leave a signature in PD (Mooers & Heard, 1997). Additionally, environmental factors that could affect PD include areas of long-term climate stability and areas with a steep altitudinal gradient, both of which could lead to areas acting as climate refugia (Keppel *et al.*, 2012) and might allow species to persist during periods of rapid climate change. Such regions have been found to correlate with species endemism and sometimes contain very old species lineages (Fjeldså & Lovette, 1997). Mountain ranges have the potential to limit extinctions by providing a high diversity of climates in a local area and, thus, providing localised climatic refugia. SR is especially strongly related to altitudinal range in warmer climates, where it creates a steeper gradient on a small scale(Janzen, 1967; Ruggiero & Hawkins, 2008). Unsurprising, mountains harbour half of the currently recognised biodiversity hotspots (Kohler & Maselli, 2009), although this might be partly an artefact, due to lower human impacts in remote mountain regions (Joppa & Pfaff, 2009). Areas such as the northern Andes still harbour ancient lineages of arctic species which have persisted since the late Pliocene or early Pleistocene (Hughes & Eastwood, 2006) and could therefore potentially harbour a high relative PD. Species in mountain ranges at lower latitudes as the tropical Andes and the Afro and Sino Himalayan montane regions, by contrast, are

suggested to have undergone high rates of speciation (Fjeldså, 2012). Relatively young mountain areas, such as the Himalayas, which are still rising a centimetre per year (Bilham *et al.*, 1997), and the central Andes, could contain recent species radiations (McGuire *et al.*, 2014) leading to a low relative PD.

Ecological transition zones, harbouring communities with great genetic diversity (Petit *et al.*, 2003) could also have higher relative PD, due to the occurrence of species adapted to different ecological zones within one community. They can be important zones of differentiation and speciation caused by species adaptations (Smith *et al.*, 1997). Transition zones are well known to harbour high species richness and biodiversity (Odum, 1971) and have been related to genetic diversity within taxa (Petit *et al.*, 2003). They can accommodate species from two or more realms, each of which may have experienced very different evolutionary histories. Hence, such regions could potentially contain high relative PD. However, high speciation rates have also been recorded in some ecological transition zones (Schilthuizen, 2000), which would result in a low relative PD.

Habitat diversity, which is known to affect SR (Rahbek & Graves, 2001) and to drive diversification (Emerson & Kolm, 2005), could also affect PD. It has been often related to SR. A study of South American breeding birds, for example, found that up to 51% percent of the variation in species richness could be explained by the number of ecosystems within a 1° grid cell (Rahbek & Graves 2001). I do expect habitat diversity to affect SR rather than PD.

Identifying regions where PD is higher or lower than would be expected given SR (PD relative to the SR within the area, hereafter termed relative PD, or rPD), and exploring environmental correlates of rPD, can help identify communities with high irreplaceability, when assessed in terms of the uniqueness of evolutionary histories.

Here, for the first time, I: (1) map geographic variation in avian rPD and identify those areas characterised by particularly high or low values; and (2) explore potential environmental correlates of PD, in addition to SR, that might indicate where the macroecological processes of dispersal and diversification differ from the global average (Fritz & Rahbek, 2012). I develop models of PD on a global scale, as well as for individual biological realms. I hypothesise that high rPD should be favoured by relatively stable climates, but that habitat diversity will principally affect SR. High rPD might also arise from opportunities for community interchange (for example at boundaries between realms), or by relative isolation (promoting the persistence of ancient lineages). Conversely, I expect lower rPD on more recently formed land-masses. I expect the drivers of PD to differ between individual biological realms, since many broad-scale, macroecological processes differ between

these geographic areas. I discuss the implications of our findings for conservation prioritisation, highlighting differences between biodiversity metrics and between major taxonomic groups.

6.3 Methods

6.3.1 Species distribution data

I estimated the extant species present in each grid cell across the global terrestrial land mass using global breeding range maps for 9227 bird species (BirdLife International & NatureServe, 2012). Taxonomic differences between the species' range data and the avian phylogeny used (see below), meant that 420 of the 9227 species were excluded, e.g. species might be recognized as one species in the phylogeny but split into two separate species in the BirdLife taxonomy. Owing to our terrestrial focus, a further 346 seabird species were also excluded. Range data were transferred onto an equal area grid in Behrman projection with a cell size of 1° latitude by 1° longitude at 30°N and 30°S latitude (Orme *et al.*, 2005; Fritz & Rahbek, 2012; Huang *et al.*, 2012). An equal area grid enables spatially unbiased comparisons among grid cells. A species was considered to occur in a cell only if the species' range polygon and grid cell overlap was ≥ 10%, a threshold that prevents species being represented in cells in which their occurrence is very limited. For 1287 species with ranges so restricted that they never occur in at least 10% of any cell, their occurrences were derived from the intersection of their range polygons with cells, without applying a 10% threshold. The gridded species' range data were then used to determine species lists for each grid cell across the globe.

6.3.2 Global phylogenetic diversity

To derive PD, I used the first full phylogeny of extant birds (Jetz *et al.*, 2012). These phylogenetic data are provided as 10,000 possible tree topologies in Newick tree format (Olsen, 1990). The phylogenetic data are available based on two taxonomic backbones: those of Hackett *et al.* (2008) and Ericson (Ericson *et al.*, 2006). Here I used the phylogeny based on the Hackett backbone, which is the more recent higher-level avian topology available (Hackett *et al.*, 2008).

Several indices are available to measure PD but the most frequently used is Faith's PD (Cadotte *et al.*, 2010). Faith's PD (hereafter just PD) summarises how much of the branching pattern of a phylogenetic tree is represented in a community, by adding the branch lengths for all members of the community (Faith, 1992). As such, it provides a summary measure of the phylogenetic diversity of a community (Faith, 1992; Barker, 2002). For each terrestrial grid cell globally, I calculated SR and PD. To aid the comparison of PD between cells, the root of the phylogenetic tree was excluded and the tree was pruned, using the 'APE' package in R (Paradis *et al.*, 2004), to the most recent common ancestor of the species within each cell (Faith, 1992). I calculated PD for all terrestrial cells containing at least two species. Grid cells that contain only one species cannot provide a minimum

spanning path between two species, resulting in the exclusion of some cells in the Saharan desert and around the poles (Faith, 1992; Barker, 2002). In total, I collected data on avian PD from 17,363 terrestrial grid cells.

A pilot study (S6.1, Figure S6.1) showed that 200 randomly chosen potential trees of the avian phylogeny (Jetz *et al.*, 2012) were adequate to reduce the coefficient of variation (from the trees available in this phylogeny) of estimated PD, for individual cells, to below 0.005 for 90% of the test cells. Consequently, I estimated PD for all cells using a random selection of 200 of the possible phylogenetic trees. Previous studies have used different methods to investigate the relationship between PD and SR, including analysing the residuals of the modelled relationship (Davies & Buckley, 2011; Fritz & Rahbek, 2012), or using a null model based on randomized species assemblages, which are then compared to the empirical data; the latter having been used only for studies on a smaller scale (Kluge & Kessler, 2011). Here, I used two approaches. Firstly, I followed the methods of Fritz and Rahbek (2012) and modelled the relationship between PD and SR using local regression with nonparametric smoothing techniques (Forest *et al.*, 2007), utilising functions from the 'CAIC' package in R (Orme *et al.*, 2009). This allows us to compare our results to previous studies on global patterns of PD that have used a similar approach but for other taxa (Davies & Buckley, 2011; Fritz & Rahbek, 2012). To highlight areas with unusually high or low rPD, I selected the cells with the top and bottom 5% of the residuals from the local regression between PD and SR (Fritz & Rahbek, 2012).

Secondly, because when using a local regression with nonparametric smoothing techniques, the residuals can be affected by the surrounding cells, i.e. the rPD value for a grid cell is always relative to the surrounding values within the window of the local regression, which could mask important general relationships, I used an alternative method to check the robustness of the observed patterns in rPD. I ordered the cells of the world by their SR values and divided them into five equal-sized groups. I fitted a generalized (Michaelis-Menten) saturating curve to the PD and SR data from a random data sample (n = 1000) drawn from each the five groups and then predicted to the four left-out groups each time. The process was repeated 50 times, taking new random samples each time. From these predictions I calculated the mean residual value from the fitted generalized saturating curves for each grid cell. Unlike in the locally-weighted regression, the resultant residual is relative to the whole dataset and not just to grid cells with similar SR values. Although the patterns of the residuals from this alternative approach (See Figure S6.2) are less pronounced than those of the locally-weighted regressions (See Figure S6.3) and the transitions between areas of low and high residual are more gradual, the overall pattern remains very similar. Consequently, and for simplicity, I display only results from the locally weighted regression analysis in this Chapter.

6.3.3 Environmental correlates of rPD

I assessed environmental characteristics that might be associated with geographic variation in rPD. Specifically, I modelled the relationship between PD and SR, including additional covariates to help explain divergence. These additional covariates were: the distance to the nearest neighbouring realm, altitudinal range (considered as a proxy for within-cell climatic diversity), climate stability since the Last Glacial Maximum (LGM, present to 20,000 years ago), climate stability since the last interglacial period (LIG, present to 125,000 years ago), and habitat diversity. The derivations of these covariates are described below.

I calculated the distance of each grid cell to the nearest neighbouring realm, based on an updated version of Wallace's zoogeographic regions of the world (Holt *et al.*, 2013), to get a value for each grid cell how far it is located from an ecological transition zone. To calculate the altitudinal range within each cell I used the 30 arc second (approx. 1 x 1 km) GMTED 2010 global elevation data (U.S. Geological Survey, 2012a). Habitat diversity was measured as the number of habitats covering a minimum of 1% of a cell's area, using the USGS vegetation cover data, which comprises 24 different habitat types (U.S. Geological Survey, 2012).

Measures of temporal climate stability for two time periods (since the LGM, and since the LIG) were based on modelled palaeo-climatic data. I explored the mean climate stability since the last glacial maximum (LGM) and the last interglacial period (LIG). The climate data were available on two different timescales. Data since the LGM (present to 20,000 years ago) were available in steps of 2000 years. Data since the LIG period (present to 125,000 years ago) were available in intervals of 4000 years. To represent overall palaeo-climate stability in each cell, I used temperature and precipitation data. I determined mean values of z-transformed temperature and precipitation data in each relevant year. For each consecutive temporal transition, I estimated the mean Euclidean distance between temperature and precipitation in bivariate space. The mean of these Euclidean distances was our measure of overall palaeo-climatic stability. Additionally, I repeated the above calculations for each cell but used the maximum Euclidean distance for the two variables, since extreme events may drive extinction (Crowley & North, 1988; Parmesan, 2006). To estimate stability in temperature and precipitation individually over time, I calculated the standard deviation within each cell for both variables for each of the LIG and LMG climatic datasets. I considered temperature and precipitation separately, as well as jointly, as their importance may differ regionally.

The palaeo-climate data were derived from a series of general circulation model (GCM) climate simulations, performed using the HadCM3 version of the Hadley Centre Unified Model (Gordon *et al.*, 2000; Pope *et al.*, 2000). Details of the model's configuration are given by Singarayer & Valdes

(2010), and the resultant climate data were made available by the Bristol Research Initiative for the Global Environment (BRIDGE, http://www.bridge.bris.ac.uk/).

I extracted, as potential explanatory palaeoclimatic variables: (1) the stability of past precipitation, (2) the stability of past temperature, and (3) a bivariate metric based on variation in both of those variables. From these I calculated eight potential palaeoclimate environmental covariates, including stability of: mean temperature, mean precipitation, mean bivariate climate and maximum bivariate climate, for time since both LGM and LIG. I used the potential for maximum values to explain PD because extreme events may drive extinctions (Crowley & North, 1988; Parmesan, 2006). Following Dormann *et al.*, (2013), I avoided combinations of highly correlated climate variables (Pearsons' correlation, $r > 0.70$). Specifically, I used a preliminary model selection approach to select the climate stability variable with the most explanatory power, such that no model contained more than one metric of climate stability. I sequentially produced models of PD including all potential response variables, but only one of the climate variables each time. For each combination of model explanators (i.e. each with a different climate variable) I used a model selection approach (Burnham & Anderson, 2002; Burnham *et al.*, 2011), calculating the mean AIC across a 1000 random subsamples (using the 'AICcmodavg' package in R; (Mazerolle, 2014). The random samples were drawn using the blocking method (described below). The climate variable contained in the model set that had the lowest mean AIC were used for all subsequent modelling.

Following preliminary data exploration, I included quadratic terms for SR, altitudinal range and climate stability variables, and linear effects for the remaining variables in our models to estimate global PD. To identify global drivers of PD, I fitted general linear models of global PD including all valid combinations of environmental covariates and polynomial terms. The PD values were highly spatially auto-correlated (Moran's I = 0.99), which can affect inference. To minimise the potential impacts of spatial autocorrelation on inference, I designed a blocking method in which models of global PD were built and tested using spatially disaggregated data (Figure S6.4). For modelling, I repeatedly drew random subsets of ten percent of the grid cells from each block, using blocks from only one of the two checkerboard groups each time (datasets were drawn equally from the two checkerboard groups). This resulted in approximately 1700 randomly selected cells being drawn broadly from across the globe, for each iteration of the global model. This approach substantially reduced the spatial autocorrelation (mean Moran's I across random data subsets = 0.18; Table 1). Using this blocking method I fitted models to 1000 random subsets of the data. In each case, I selected among all competing models using the 'MuMIn' package in R (Barton, 2014). Inevitably, this resampling approach resulted in subtly different variable selection for each random subset of

data. To identify those parameters with robust and repeatable influences on PD, I recorded the frequency with which individual environmental covariates were selected in the top models across the 1000 subsets. I report the parameter values for those covariates that were included in at least 95% of the top models (Figure S6.5). Parameters defined as robust by this method were used to predict PD for all terrestrial cells globally.

To test whether environmental covariates relate to PD in different ways, or to differing degrees, in individual biological realms, I produced models similar to the global models described above but fitted instead to data from the individual realms. I considered only those realms with > 500 grid cells, to permit a blocking approach during model fitting. Eight realms satisfied this selection criterion: the Afrotropical, Neotropical, Nearctic, Australian, Saharo-Arabian, Sino-Japanese, Oriental and Palaearctic realms. Each of these realms was split into eight blocks, using the same method as for the global model. Following the same approach as described above for the global data, I identified the best model for each biological realm.

For each of the identified best models for the global scale and the individual biological realms, I calculated McFadden's r^2 (McFadden, 1974; Beaujean, 2012) as a measure of the extent to which the model with the lowest Akaike information criterion (AIC) value was an improvement over an alternative model containing only SR. Finally, I compared the predictions of PD from the global model with the predictions of the models based on the individual realms to assess whether the improvement in predictions of PD based on combining predictions from models fitted to the individual realms justifies the increase in complexity over the model fitted to the global data. To do this, I compared the AIC (based on the least squares case, Burnham & Anderson, 2002, p.46) of the global model to that of an amalgamation of the separate realm predictions, for the realms where I could produce estimates using both methods.

6.4 Results

Global patterns of SR, PD and rPD

As expected, the correlation between SR (Fig. 1a) and PD (Fig. 1b) is very high for terrestrial bird species across the globe (Fig. 2a; $r^2 = 0.973$). Nonetheless, the residuals of the LOESS regression have a marked spatial pattern (Fig. 1c, 1d), with clusters of positive and negative residuals that indicate divergence between SR and PD (Fig. 2b). Areas with the most negative rPD (i.e. where PD is lower than expected given SR) include areas of high relief, such as the Himalayas and Andes, and also areas of glacial coverage during the LGM, such as the northern Nearctic and Palaearctic. Extensive areas of high rPD occur on isolated tropical islands including Madagascar and Sri Lanka, and in dryland areas fringing the subtropics. The latter regions include the Sahelian edge of the Afrotropical realm, parts of eastern Africa and central southern Africa, as well as northern Australia and the border between India and Pakistan.

Potential drivers of avian PD

The best global model of avian PD included the variables SR, mean climate stability since the LIG and altitudinal range, and explained 98% ($r^2 = 0.982$, Table 1, Table 2) of the variation in PD. This model explained one third of the remaining variation in PD when compared to the global model including only SR ($r^2 = 0.973$, Table 1).

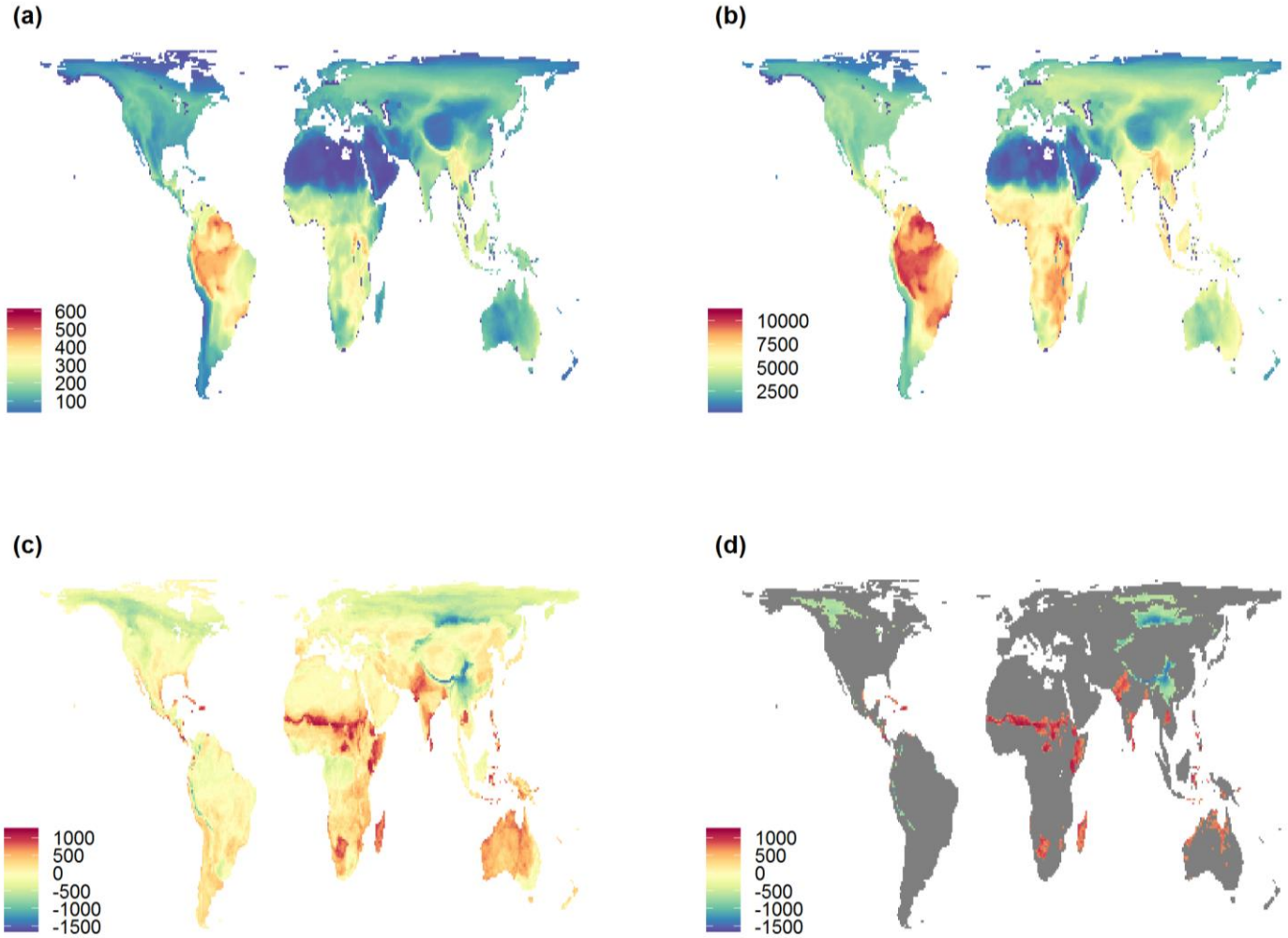

Figure 1: Global maps (Behrman projection) showing (a) global avian species richness, (b) global avian phylogenetic diversity (calculated using Faith's (1992) phylogenetic diversity), (c) residuals of the local regression (LOESS) between avian species richness (SR) and phylogenetic diversity (PD) and (d) global areas containing the highest or lowest 5% of the residuals, with cells that do not fall in the top or bottom 5% masked in grey. In the latter two graphs, red indicates unusually high PD given the SR, and blue unusually low PD given the SR.

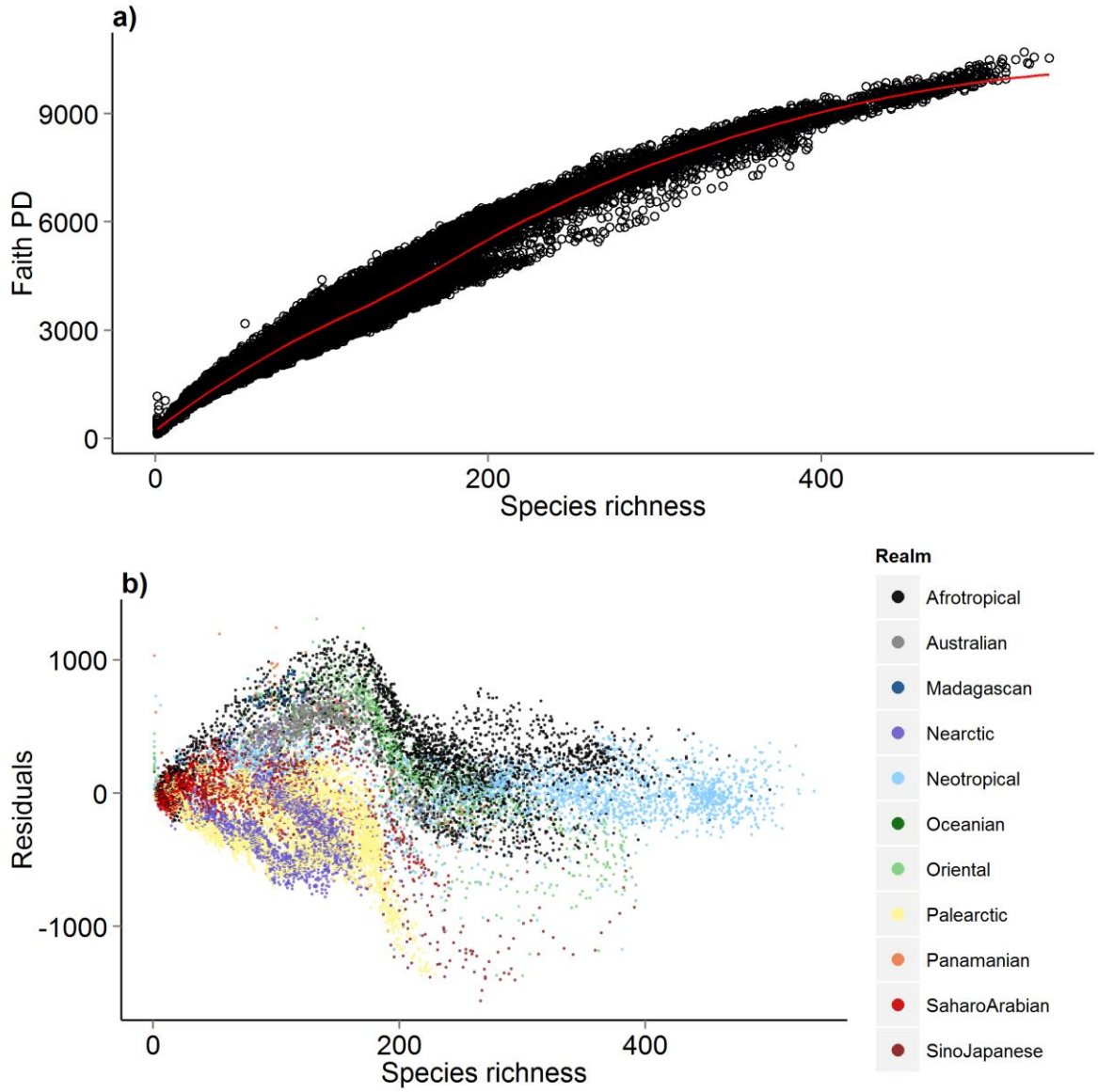

Figure 2: (a) The global relationship between avian species richness (SR) and phylogenetic diversity (PD); the red line was fitted to the data using local regression with nonparametric smoothing techniques; (b) residuals of the local regression plotted against avian species richness, coloured by realm.

At a realm level, the climate variables included in the best model of PD differed among realms (Table 2). Nonetheless, for all realms, besides the Australian and the Neotropical realm, the best PD models included one of the LIG climate variables. Other variables (apart from SR and climatic variables) included in the best realm models of PD were the distance to the nearest neighbouring realm and altitudinal range, though combinations of variables in the best individual realm models differed. For the Oriental and Saharo-Arabian realms, no additional drivers of PD could be identified in addition to SR.

Overall, the amalgamated realm level models described PD better than the global level model (realm model AIC: 81420, global model AIC: 86716). The residuals of the realm level models (Fig. 3b) have a considerably less pronounced pattern than the residuals of the global level model suggesting that these models are able to explain considerably more of the divergence between PD and SR than the global model (Fig. 3a).

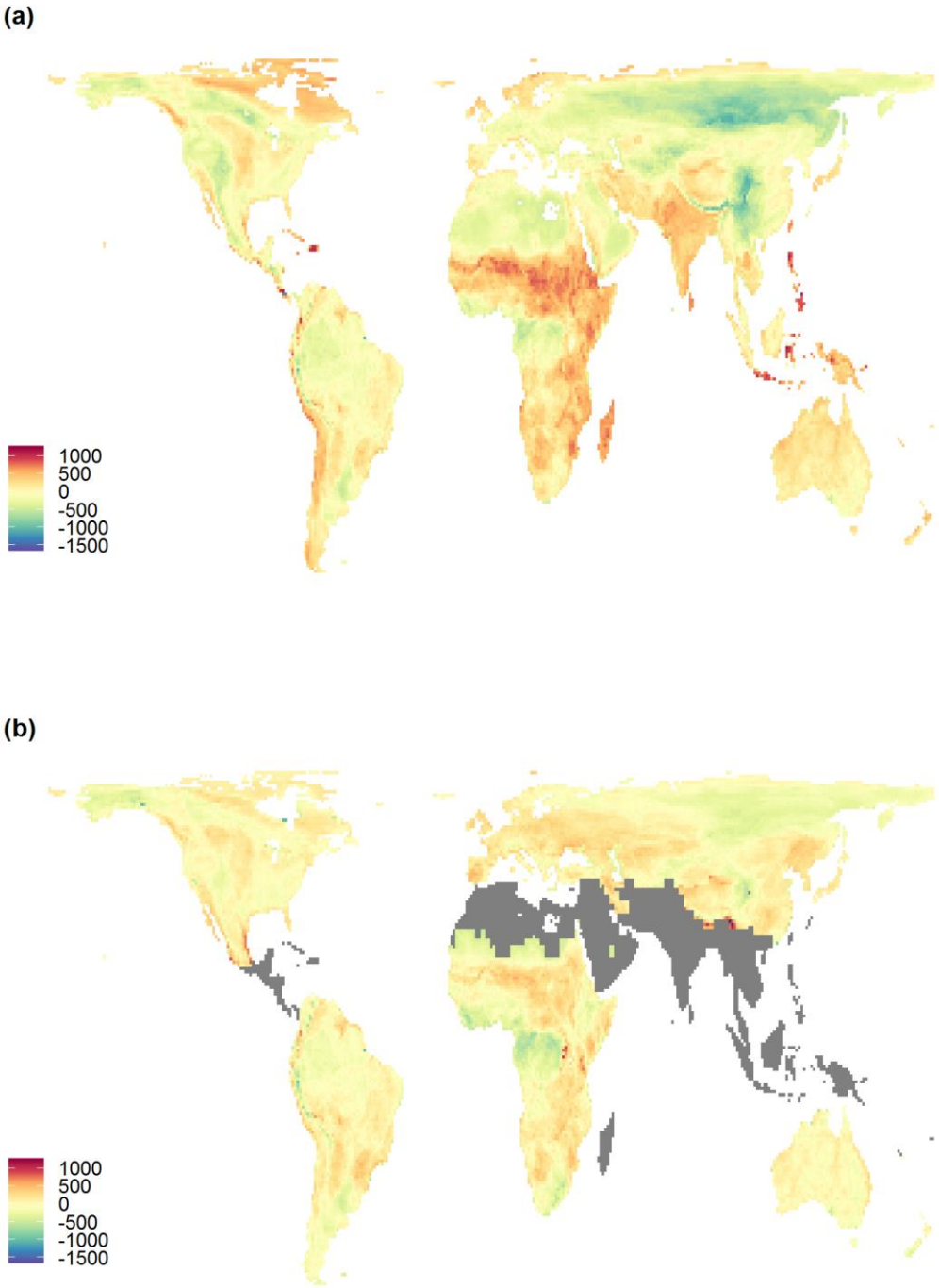

Figure 3: (a) The residuals of the global model to predict phylogenetic diversity (PD) and (b) the residuals of stitched models per realm. Realms with less than 500 cells and realms where no drivers for the PD pattern other than species richness (SR) could be identified were excluded from the individual realm analysis and are masked grey.

Table 1: Variables used to model phylogenetic diversity on a global scale and in the individual realms. Coefficients are given for all variables that have been used in a model. Variables which have been consistently selected for the best model (variables that were in the best model after model selection 95% of the time) are highlighted in grey. Variables which have not been used in any of the models were excluded from the table (Habitat diversity, Mean long-term climate stability, Mean short-term climate stability, Max-short term climate stability, Short-term Temperature stability). All variables besides Distance to the nearest neigbouring realm were included with quadratic terms.

	Global	**Afrotropical**	**Australian**	**Neotropical**	**Nearctic**	**Palearctic**
Distance to nearest neighbouring realm	-0.010	-0.050	-0.044	0.023	0.075	-0.057
Altitudinal range	-0.041	-0.017	-0.021	-0.035	-0.116	-0.059
Altitudinal range	0.005	0.001	0.007	-0.006	0.081	0.028
Max long term climate stability	-	-	-	-	-0.267	-
Max long term climate stability	-	-	-	-	0.080	-
Long term precipitation stability	-	-0.025	-	-	-	-
Long term precipitation stability	-	0.011	-	-	-	-
Short term precipitation stability	-	-	-0.013	-	-	-
Short term precipitation stability	-	-	0.022	-	-	-
Long term temperature stability	-0.079	-	-	-0.009	-	-0.071
Long term Temperature stability	0.044	-	-	-0.010	-	0.068
Species richness	0.955	1.004	0.987	0.975	0.938	0.985
Species richness	-0.141	-0.181	-0.083	-0.131	-0.055	-0.060

Table 2: Mean autocorrelation values (Moran's I) for the model fitting data after subsampling and r^2 values for the species richness (SR) only model and the full model (SR plus the additional explanatory variables) for the global scale model and the individual realm models (same as Table 1).

	Morans I	**r^2 null model**	**r^2 full model**
Global	0.180	0.973	0.984
Afrotropical	0.183	0.980	0.990
Australian	0.156	0.913	0.988
Nearctic	0.154	0.900	0.954
Neotropical	0.175	0.937	0.946
Palearctic	0.165	0.965	0.971

6.5 Discussion

6.5.1 Global patterns of avian rPD

Our analyses show that macro-evolutionary processes have left a strong pattern in the phylogenetic diversity of current avian assemblages. I have shown that there is clear spatial patterning in areas where PD diverges from SR, and this suggests that biological and geological processes play a major role in rPD. The spatial pattern observed here for birds differs markedly to those that have been observed previously for other taxa (Davies *et al.*, 2008; Davies & Buckley, 2011; Fritz & Rahbek, 2012), indicating that these processes may operate differently across taxonomic groups. Areas of low avian rPD occurred at high latitudes and in areas of high relief associated with the Andes and Himalayan mountain ranges. Areas with particularly high rPD were distributed more widely and include islands and isolated regions, such as Australia and Madagascar, as well as ecological transition zones, such as the Sahel and parts of Central America.

I discuss the results in the context of the correlates of rPD identified in this study; the relationship between avian, mammalian and amphibian rPD; the importance of refining our understanding of rPD; and the potential implications for conservation.

6.5.2 Potential drivers of avian PD

As suggested by earlier studies (Rodrigues *et al.*, 2005; Davies & Buckley, 2011; Fritz & Rahbek, 2012), SR showed a high correlation with PD; however, additional variables explained much of the remaining variation (rPD). As expected, the importance of the additional environmental variables differed between the individual realms and, consequently, the individual realm models predicted realm-level PD better than a single global model. Areas of very high or low rPD reveal information about the underlying structures of the communities, and indicate if these are taxonomically clustered or over dispersed (Rodrigues *et al.*, 2005; Forest *et al.*, 2007). Unusually high rPD, i.e. a taxonomically over-dispersed assemblage in an area, especially when associated with low SR, can be the result of the existence of old lineages, harbouring unique evolutionary information. These lineages can result from a speciation process with little radiation, or from the extinction of other species in the same clades (Rodrigues *et al.*, 2005). These old lineages occur more frequently in the Neotropical and Afrotropical regions, which harbour large numbers of basal taxa (Wiens & Donoghue, 2004; Hawkins *et al.*, 2006; Hawkins *et al.*, 2007). By contrast, unusually low rPD (i.e., a taxonomically clustered assemblage) is more likely to occur in areas with more recent speciation events (Davies & Buckley, 2011).

The environmental predictors tested here were expected, *a priori*, to be important based on macroecological and biogeographic theory. For example, contact zones between realms could

positively affect the rPD, because dispersal events from different species pools in neighbouring biogeographic realms into areas in the contact zone are likely to occur. I found that a large proportion of the cells with a high rPD are located within contact regions between biomes, such as in Sahelian Africa. Consequently, the distance to the nearest neighbouring realm was an important driver of the rPD pattern in the Afrotropical realm.

Another likely predictor of low rPD that I considered *a priori* was climate stability. It was selected because areas with unstable climates are likely to experience frequent local extinction events, reducing the number of old lineages. The largest clusters of low rPD occur in the two large northern-temperate realms, as well as in some mountain areas at lower latitudes, such as occur in the Andes and the Himalayas. In the Nearctic and Palaearctic, the climatic stability since the LIG is the most important explanatory variable of rPD. Low rPD in areas of climatic instability since the LIG might reflect the impact of past glacial events, and result in a phylogenetically depauperate fauna considering the SR in the area.

Altitudinal range was considered a potential driver of both high and low rPD, depending on the age of the mountain range and the local climate stability. High rPD is likely to occur where movement up or down the altitudinal gradient could act as a local buffer against climatic variation, enabling persistence of lineages. Low rPD is likely to be found where mountain ranges are relatively young and provide a centre for relatively recent speciation events. Previous studies have identified mountain ranges as centres for speciation during the Pleistocene period (circa 2.5Ma to 12Ka) (Fjeldså, 2012; Päckert *et al.*, 2012), although there is evidence that some of the younger mountain ranges are approaching ecological saturation and species radiations are slowing down (Price *et al.*, 2014). I found greater support for altitudinal range being associated with low rPD, with areas of low rPD in the relatively young Andes and Himalayan mountain ranges. The importance of altitudinal range in explaining rPD in the Neotropical realm model, which contains the Andes, similarly suggests that these mountain ranges may act as centres for recent speciation, resulting in low rPD despite high endemism. Hence, the variables that best explained rPD in this study tend to fit with contemporary evolutionary and geological understanding of how species have evolved and persisted.

The only potential driver of avian PD that was not selected as important in any model was contemporary habitat diversity. This might reflect that habitat diversity mainly drives patterns of SR (Lack, 1969; Bazzaz, 1975). It might also arise because of the use of contemporary habitat diversity data, which does not reflect long-term changes in habitat diversity that might have influenced the current PD pattern.

Several of the larger biological realms span multiple ecosystems, such that variables explaining rPD may not operate similarly across the entire area. As I only report variables that are selected in most models, this could result in some important variables that operate in only part of a realm being overlooked. For example, in the Oriental realm, only SR was consistently selected, although long term temperature stability was selected in 76% of models explaining PD. I found that adding this variable significantly improved PD prediction for the Indian subcontinent but not for the rest of the Oriental realm. This suggests that, for some realms, variables influencing PD may be operating over a finer scale than the realm and conducting analyses over smaller sub-regions could highlight locally influential variables that are overlooked by our realm-level analysis.

6.5.3 Mismatch of avian rPD with that of other taxa

The rPD patterns found for birds are very different from those previously identified for amphibians (Fritz & Rahbek, 2012) and mammals (Davies & Buckley, 2011; Safi *et al.*, 2011; Rosauer & Jetz, 2015). Strikingly, the patterns of highest and lowest rPD for birds are, to a large extent, the inverse of those found for amphibians. In particular, for birds, areas of low rPD are often located in extensive mainland areas and in mountainous areas such as the Himalayas and the Andes; for amphibians these are areas of high rPD. For amphibians, islands and isolated areas such as Australia, Madagascar, New Guinea and the Caribbean have been identified as having low rPD (Fritz & Rahbek, 2012), whereas for birds these tend to be regions of high rPD. Similarly, areas of high rPD for amphibians in the Indo-Chinese realm are identified as regions of lower than expected PD for birds. For birds and mammals, there are also areas where the two taxa show contrasting patterns of rPD. This occurs in islands and isolated areas such as Australia and the Caribbean, as well as Central America, with avian rPD being higher than mammal rPD. Areas such as the Sahel, parts of Eastern and Southern Africa, and parts of the Indian subcontinent show a high rPD for both taxa.

Relatively few areas of the world have similarly high rPD for birds, mammals and amphibians. Those that do include parts of South America which lie to the east of the Andes, the Cameroon Highlands and parts of the Eastern Arc mountain range in Africa. Amphibians and birds also both have high rPD in SE Brazil and parts of Indochina. However, outside of Amazonia, the most remarkable thing about rPD patterns of these taxa is their lack of congruence. This may, in part, be a result of the mobility of birds relative to mammals and amphibians, which could facilitate relatively rapid recolonization of newly exposed mountain and arctic sites following glaciation events, and increased colonisation of isolated island sites (Weir & Schluter, 2004). It could explain the different observed patterns among taxa on islands and newly exposed sites, which often show very low rPD for amphibians and mammal but not for birds.

6.5.4 Improving our understanding of rPD

Here, I try to explain rPD through consideration of contemporary niche diversity (current habitat and climate diversity) and longer term climate stability. However, there are other potentially important determinants of PD that I was unable to consider, including short duration extreme events (climatic or tectonic), longer term habitat occurrence and persistence, and isolation/connectivity due to landmass movements. One of our putative niche measures, elevation range (considered a proxy for contemporary climate diversity), may have operated more as a tectonic proxy in our models, by highlighting the youngest land on mainland landmasses, such as the Himalayas and Andes. Assessing directly the role of these longer-term landmass and habitat changes and the impacts of extreme events was not possible in the current study. Future studies of PD would undoubtedly benefit from the inclusion of such measures, should data become available.

The phylogeny of Jetz *et al.* (2012) is the best full avian phylogeny currently available. Nevertheless, it has been the focus of academic discussion as a result of the methods used to construct the phylogenetic tree (Ricklefs & Pagel, 2012). Using a previously defined backbone (which included 158 major bird clades in the case of the backbone based on Hacket et al. (2008) that I used) to define the tree's outline might result in restricted variation in higher order relatedness between avian species. It is possible that avian evolution might be better described by another tree (Ricklefs & Pagel, 2012), and amendments to phylogenetic trees are frequently proposed. Furthermore, the uncertainty around estimating branch length, inferred from time-dated trees (Venditti *et al.*, 2010), can introduce additional bias (Ricklefs & Pagel, 2012). Spatial differences in the degree to which bird populations are distinguished at the species level contribute another potential source of uncertainty. Areas such as North America and Europe, with finely distinguished populations, may contain artefactually inflated species diversification compared to areas with less resolved populations (Ricklefs & Pagel, 2012). All three of these sources of uncertainty could affect the total branch length calculated for a community and, therefore, affect the observed pattern of avian PD.

Amendments to the avian taxonomy are ongoing, and suggested alterations to the phylogeny of living birds further our understanding of avian phylogenetic history. Recent amendments demonstrate the rapid advances in this field (Jarvis *et al*. 2014, Prum *et al.* 2015, Rocha *et al*. 2015). Repeating our analyses with alternative full avian phylogenies, when available, will determine how robust the patterns identified here are to updates in taxonomy. For instance, the recently published genomes of 48 species representing all Neoaves by Jarvis et al. (2014), resulted in a rearrangement of some of the early branches in the tree of life. Since then, Prum et al. (2015) have published a comprehensive phylogeny, based on more species (198) but sampling only genetic regions rather than whole genomes. The latter contradicts some of Jarvis et al.'s (2014) findings, as with, for

example, the splitting of Neoaves into five rather than two groups. Advances are also continuously made on subsets of the avian phylogenetic tree (e.g. (Rocha *et al.*, 2015)). Such work will inevitably lead to a more accurate tree of all living birds, which will refine the observed global geographic patterns of avian PD and rPD. The backbone that I used in this study (Hackett et al. 2008) is broadly similar to the most recent phylogeny of Prum et al. (2015) for terrestrial birds (our focal species). Moreover, among the many possible trees that the phylogeny of Jetz (2012) produces, variance in PD resulting from applying different potential trees was small (Figure S6).

Our study gives a first indication of the variables that drive avian rPD patterns on a large scale in different ecoregions of the world, and identifies areas where macro-ecological processes are likely to have affected the underlying structures of species in a community, resulting in a mismatch between SR and PD. Future work could focus on understanding the causes of pattern in rPD at a finer scale. Exploring beta diversity (Whittaker, 1960) across areas with a steep rPD gradient could aid our understanding of how changing species compositions affect rPD, and enable deeper insights into the drivers at a local scale. For example, high rPD might be primarily driven by the occurrence of a small number of old lineages in an area.

Studies considering PD for conservation purposes have become more frequent (Rodrigues & Gaston, 2002; Winter *et al.*, 2012; Brooks *et al.*, 2015). These have advocated, for example, conservation that prioritises the protection of unique lineages (Isaac *et al.*, 2007). Nonetheless, phylogenetic information remains under-used (Rodrigues *et al.*, 2011). One difficulty is that biodiversity measures based on phylogenetic information [e.g. PD (Faith, 1992), phylogenetic endemism (Rosauer *et al.*, 2009), and evolutionary distinctiveness (Isaac *et al.*, 2007)] have been found to be inconsistent in their spatial congruence (Daru *et al.*, 2014). A future research priority should be to improve our understanding of the global pattern of rPD among taxa and its relationship with other biodiversity measures, and with current protected area networks, to make phylogenetic information more applicable for conservation practice.

6.5.5 Implications for conservation

Our findings have implications for biodiversity conservation. Aside from the role of rPD in aiding our understanding of historical patterns of evolution, extinction and colonisation, rPD could prove a useful metric to highlight areas of high irreplaceability and added value, in conservation terms. Our study confirms that, across much of the world, SR provides a good proxy for avian PD and, hence, provides a good surrogate for biodiversity (where biodiversity is richness at all diversity scales, including phylogenetic diversity). However, I also identify areas of high (or low) rPD where this relationship is weaker. The areas of high rPD are of particular interest for conservation planning

since they indicate a likely high evolutionary potential of a community, in comparison to communities with a similar SR in combination with an average or low rPD value. Interestingly, for birds, I find that many areas prioritised because of endemic species actually have low rPD. Typically, these areas are associated with recent species radiations as seen in, for example, the Andes which have a comparably low rPD. This region harbours many endemic, but closely related, hummingbirds (McGuire *et al.*, 2014). Consequently, such areas might be considered of lower conservation priority than regions with similar SR but higher rPD.

Importantly, the lack of overlap between the rPD of birds, amphibians and mammals, compels caution in generalising PD results among taxa. This result is consistent with a recent study by Zupan *et al.*, (2014) which suggests strong divergence between the patterns of PD in vertebrate taxa across Europe. As with SR, it seems that there is no 'silver bullet' indicator taxon that can be used to infer PD across taxa. That habitat diversity was seldom identified as a useful predictor of PD suggests that this, too, would be a poor metric of current PD. Using ecosystem-based metrics (such as habitat/ecosystem richness) as a basis for protecting areas for biodiversity conservation (Brooks *et al.*, 2006) may conserve ecosystem function, and to some extent SR, but would perform rather poorly in representing rPD, as habitat diversity was not included in our global or regional models of PD. Current best-practice to identify terrestrial biodiversity hotspots (such as Conservation International's hotspots or BirdLife International's EBAs) consider endemism but do not yet account for phylogenetic uniqueness. The next challenge for conservation biologists is to combine supertree PD data across a number of key taxa to identify hotspots of biodiversity that represent areas of true phylogenetic diversity and uniqueness, in addition to species diversity, endemism and distinctiveness.

Chapter 7:

General discussion

7. 1 Discussion

The principal motivation of this thesis was to assess the impacts of climate change on the spatial distributions of the world's terrestrial birds, identifying global trends in range-shifts and hotspots where species are projected to be most affected by climate change. I provided a first global overview of the influence of climate change-driven range changes on terrestrial birds, in terms of 1) their extinction risk, 2) their community compositions, 3) the coverage provided to avian biodiversity by the global Important Bird Area (IBA) network, and 4) identifying species that are unlikely to persist under climate change without direct conservation interventions such as Assisted Colonization (AC). Finally, I assessed the ability of species richness (SR), as a measure for biodiversity, to account for avian phylogenetic diversity (PD) on a global scale. Below, I will briefly summarize the main findings of this research, their significance for conservation and their wider relevance to the understanding of the impacts of climate change on biodiversity.

7.2 Global trends

Despite the necessary simplifications of global scale analyses, large scale studies have been able to detect general trends in species' range changes (Araújo *et al.*, 2011). The results presented in this thesis quantify, for the first time, the threat climate change poses to the world's terrestrial birds. In **Chapter 3** I showed that, as a result of climate change, about 80% of the world's terrestrial bird species are projected to experience range changes of greater than 10% of their current range. One fifth of the modelled species were predicted to experience major range losses, losing more than 75% of their current ranges. Although there was spatial patterning in these results, with high numbers of species experiencing major range changes in the tropics and at high northern latitudes, impacts of climate change on species ranges were evident throughout the globe. As a result of range changes, projected changes in community composition were similarly widespread globally, with novel communities predicted to occur within all biological realms. These results have strong relevance to conservation, highlighting the substantial overall threat that climate change poses to the world's terrestrial birds and, consequently, the urgent need for conservation interventions to mitigate impacts of climate change on these species. In particular, the high projected levels of global species turnover dovetail with findings from regional-scale studies (Stralberg *et al.*, 2009); the appearance of novel species communities across the globe poses a unique challenge for conservation. Overall, results for the world's birds are consistent with those detected in a variety of taxa, highlighting the ubiquity of the overall threat climate change poses to biodiversity via the increased risk of extinction and the potential reshuffling of global communities (Parmesan *et al.*, 1999; Parmesan & Yohe, 2003; Thomas *et al.*, 2004; Chen *et al.*, 2011).

7.3 Species conservation Protected Areas and Assisted Colonization

The results presented in **Chapter 4** show that, due to the projected impacts of climate change on species' ranges throughout the globe, a global network of protected areas (PAs) for avian biodiversity – Important Bird Areas (IBAs) – will experience high levels of turnover in avian communities. There were spatial patterns in turnover, with clusters of PAs being similarly affected. These included clusters of high turnover in southern Europe and high numbers of colonizers within the northern Palearctic. Intriguingly though, areas of exceptionally high or low turnover were not restricted to certain latitudes, being found across all biological realms. Climate change is, thus, projected to affect the performance of PAs throughout the globe. Evaluating spatial variation in the performances of PAs across networks, such as IBAs, is crucial for guiding conservation decision making (e.g., replacing poorly performing PAs) (Fuller *et al.*, 2010; Alagador *et al.*, 2014), or for the prioritization of PAs that remain valuable or increase in value (Hannah *et al.*, 2002). The results of this analysis highlight the widespread threat posed by climate change to the performance of global PA networks, illustrating the inadequacies of current PA networks to deal with climate changes and emphasising the urgency of developing improved climate change mitigation strategies. However, **Chapter 5** revealed that, even if PAs were designed taking into account the projected effects of climate change, it would not be enough to lower the extinction risk for many of the world's terrestrial birds. This analysis identified that a large number of species (about 1/8 of those modelled) are projected to experience severe enough range losses to be highlighted as potential candidates for assisted colonization (AC). These results show that, while controversial (McLachlan *et al.*, 2007; Hoegh-Guldenberg *et al.*, 2008; Ricciardi & Simberloff, 2009a), AC could be the only hope for the long-term survival of a substantial number of species. AC thus has the potential to be a valuable tool for conserving species under climate change. This analysis highlights the urgent need for further assessments and rigorous tests of this conservation tool.

7.4 Measuring avian biodiversity

The selection of appropriate measures of biodiversity is crucial for accurately assessing and mitigating for the impacts on species' communities of threatening processes such as climate change. The development of improved measures of biodiversity for conservation planning has been widely discussed (Faith *et al.*, 2004; Winter *et al.*, 2012); the use of different measures when setting conservation targets and optimizing protected area coverage can lead to contrasting priority areas (Devictor *et al.*, 2010; Daru *et al.*, 2014). Incorporating phylogenetic diversity (PD) into conservation planning could improve upon current species richness (SR) based metrics, by providing information about the functional diversity and evolutionary potential of an ecological community. In **Chapter 6** I demonstrated that, at a global scale, SR is generally a good surrogate for PD. However, at finer

scales, localized differences are evident, suggesting that PD provides more information in such areas. This is largely consistent with previous studies on other taxa (Davies & Buckley, 2011; Fritz & Rahbek, 2012), highlighting the potential importance of PD for conservation planning. Further research is required to develop strategies for the inclusion of PD in conservation planning. Importantly, the regions of relatively high PD for terrestrial birds identified here do not mirror the patterns observed for mammals and amphibians, showing that there is no 'silver bullet taxon' that can act as an indicator for important areas for PD across taxa.

7.5 Future work

The projected changes in spatial patterns of terrestrial bird ranges, and the first assessment of the effects this has on avian communities and on the protected area networks, provides a good benchmark for further research. New analyses are already under development to enhance the insights gained in this thesis and to allow more accurate projections to be made. Below, I will briefly outline some of this work.

Refining the used dispersal estimates

Accurate estimates of species' dispersal are important for projecting species' range shifts under climate change (Jaeschke *et al.*, 2013). Current dispersal estimates – as used in the SDMs in this thesis – provide more realistic projections than simple assumptions of either no dispersal or full dispersal (Araújo *et al.*, 2006; Thuiller *et al.*, 2006). However, the estimates used here are generally thought to be at the upper end of the realized dispersal potential of the terrestrial bird species. Firstly, these dispersal estimates do not take into account any reductions in dispersal speed that species will experience due to changes in biotic interactions (Urban *et al.*, 2012) and, secondly, they are not influenced by landscape permeability (Schloss *et al.*, 2012) or other barriers to dispersal. The first point is a recognized weakness of SDMs, but developing models to incorporate biotic interactions for > 9000 species is, currently, an unrealistic undertaking. The second point, however, can be addressed; in particular, I plan to develop future analyses using annual dispersal estimates, which are affected by barriers such as water bodies and gaps between mountain ranges, rather than single maximum dispersal estimates per species. This will enable the use of more realistic dispersal scenarios in climate change projections.

Incorporating future land use change

The projected species distributions in this thesis reflect the impacts of climate change on species distributions regardless of changes in land-use. Nevertheless, land-use change is a major threat to biodiversity (Vitousek *et al.*, 1997; Hoffmann *et al.*, 2010), which can amplify the impact of climate change (Oliver & Morecroft, 2014) and which, in areas such as the tropics, could outweigh the threat of climate change for species (Jetz *et al.*, 2007). The lack of available future land-use data matching

the Global Climate Models (GCMs) from the Fifth Assessment report, at the time that the climate change projections in this thesis were conducted **(Chapter 3)**, precluded the consideration of land-use in this study. **Chapter 5** includes the use of current habitat to identify species' suitable habitat and climate space; this gives a first indication of the potential suitable habitat and climate space available across species. However, using only current habitat data could influence predictions in two ways: i) habitat that is currently available might be lost through land use change by 2050, or ii) vegetation might respond to climate change and the suitable habitat for a species could have a larger extent than assumed in projections. In future analyses, I will include future land-use change – to refine species distribution projections.

Coverage provided by the IUCN recognized PA network

In this thesis, I assessed the effect that climate change has on the ability of the IBAs to conserve the world's terrestrial birds, identifying those PAs likely to experience lower or higher species turnover due to climate change. The next step, which is already underway, is to extend this analysis to include all protected areas that are categorized by the IUCN, with the goal of the comparing the coverage of this more comprehensive existing PA network with an idealized PA network. The inclusion of land-use change should further refine the range-shift projections of the world's terrestrial birds across these PAs, resulting in more accurate projections of emigration and colonisation of species within individual PAs.

Future coverage of PD

The analysis of the global relationship between PD and SR encourages further research on this topic. If PD is to be included in conservation planning, it is critical to understand how PD patterns might be influenced by climate change. Furthermore, it would also be important to identify how much of the PD of the world's terrestrial birds is currently covered by the PA networks. Overall, myriad questions emerge from the analysis in **Chapter 5**. Is PD currently under represented in PAs? How will projected range changes impact the global PD pattern? Will the high turnover projected in many PAs across the globe affect PD (e.g., would lower PD in the affected PAs be due to the processes of emigration, colonisation and extinction within these areas)? Newly available mega-phylogenies enable us now to explore these questions on a global scale (Roquet *et al.*, 2013).

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9. Supplementary material Chapter 2

Table S2.1: Bio climatic variables not selected to be tested in different variable combinations for global SDMs.

Bioclimatic variable	**Why not selected**
BIO 1 Annual mean temperature	Correlated with all other temperature variables (BIO4 – BIO11 >0.7)
BIO 2 Mean diurnal range	Correlates with BIO5 (>0.7)
BIO 3 Isothermality	(=BIO2/BIO7) Correlates BIO4, BIO6, BIO7, BIO9, BIO11 (>0.7)
BIO 7 Temperature annual range	(=BIO5-BIO6), correlates with BIO4, BIO6, BIO9, BIO11 (>0.7)
BIO 8 Mean temperature wettest quarter	Correlates with BIO5, BIO6, BIO10, BIO11 (>0.7)
BIO 9 Mean temperature driest quarter	Correlates with BIO4, BIO5, BIO6, BIO7, BIO10, BIO11 (>0.7)
BIO 10 Mean temperature warmest quarter	Correlates with BIO5, BIO6, BIO8, BIO9, BIO11 (>0.7)
BIO 11 Mean temperature coldest quarter	Correlates with BIO4 - BIO10 (>0.7)
BIO 13 Precipitation of wettest period	Correlates with BIO12, BIO16, BIO18 (>0.7)
BIO 14 Precipitation of driest period	Correlates with BIO12, BIO17 (>0.7)
BIO 16 Precipitation of wettest quarter	Correlates with BIO 12, BIO 13, BIO 18 (>0.7)
BIO 17 Precipitation of driest quarter	Correlates with BIO12, BIO14, BIO19 (>0.7)

Table S2.2: All possible variable combinations tested in the models.

Variable combinations	
Three variables	Four variables
BIO4+BIO12+BIO15	BIO4+BIO15+BIO18+BIO19
BIO4+BIO15+BIO18	BIO4+BIO5+BIO12+BIO15
BIO4+BIO15+BIO19	BIO4+BIO5+BIO15+BIO18
BIO4+BIO18+BIO19	BIO4+BIO5+BIO15+BIO19
BIO4+BIO5+BIO12	BIO4+BIO5+BIO18+BIO19
BIO4+BIO5+BIO15	BIO5+BIO15+BIO18+BIO19
BIO4+BIO5+BIO18	BIO6+BIO15+BIO18+BIO19
BIO4+BIO5+BIO19	
BIO5+BIO12+BIO15	
BIO5+BIO15+BIO18	
BIO5+BIO15+BIO19	
BIO5+BIO18+BIO19	
BIO6+BIO12+BIO15	
BIO6+BIO15+BIO18	
BIO6+BIO15+BIO19	
BIO6+BIO18+BIO19	

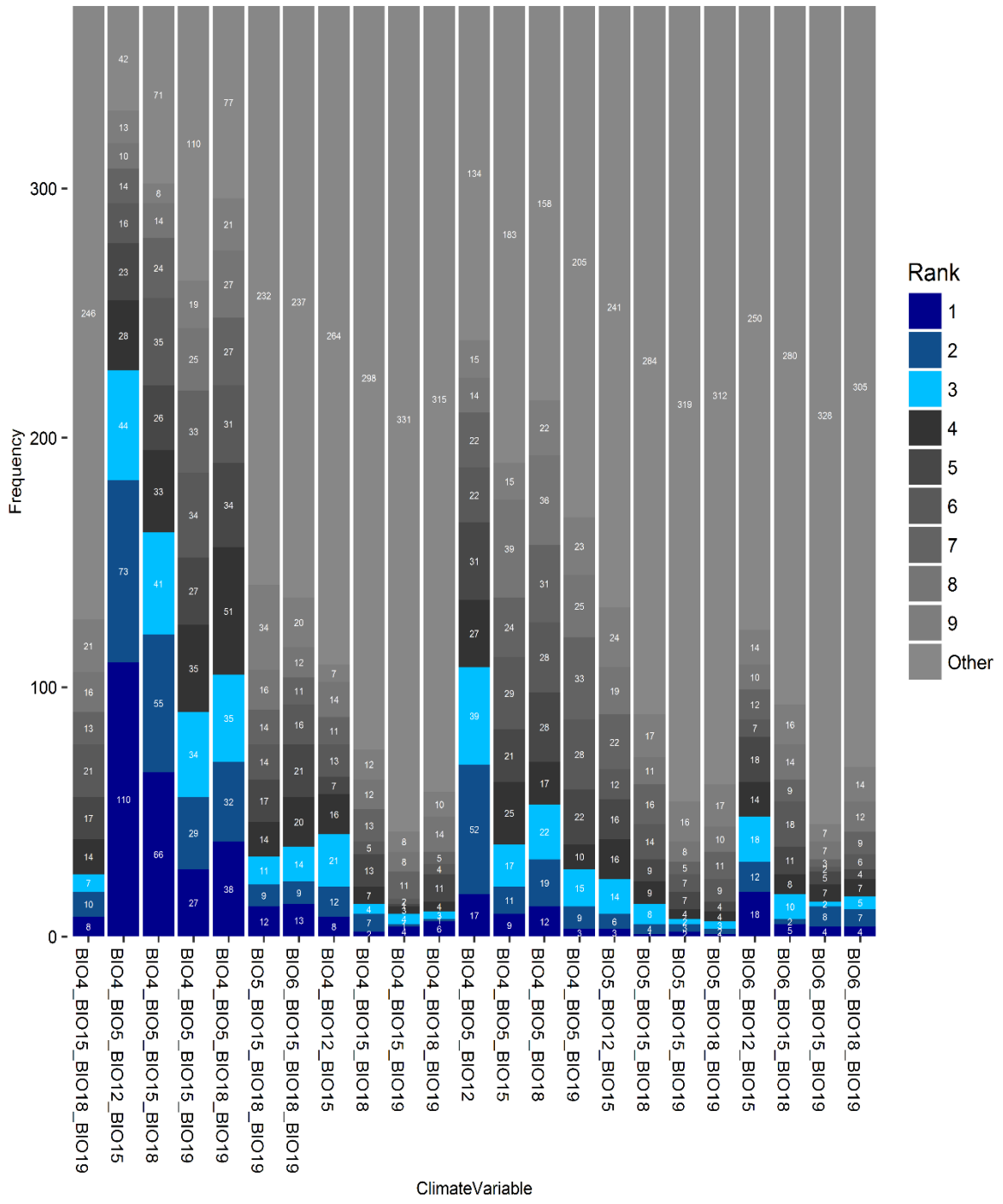

Figure S2.2: Overall ranking of the variable combinations showing results for all variable combinations.

Table 2.3: Variable importance across all 400 modelled species.

Combination	AUC	BIO4	AUC change	BIO5	AUC change	BIO6	AUC change	BIO12	AUC change	BIO15	AUC change	BIO18	AUC change	BIO19	AUC change
BIO4.BIO15.BIO18.BIO19	0.83	*	-	-	-	-	-	-	-	0.81	-0.02	0.80	-0.03	0.82	-0.01
BIO4.BIO5.BIO12.BIO15	0.87	0.83	-0.04	0.82	-0.05	-	-	0.84	-0.03	0.85	-0.02	-	-	-	-
BIO4.BIO5.BIO15.BIO18	0.86	0.82	-0.04	0.82	-0.04	-	-	-	-	0.85	-0.01	0.84	-0.02	-	-
BIO4.BIO5.BIO15.BIO19	0.85	0.81	-0.04	0.80	-0.05	-	-	-	-	0.84	-0.01	-	-	0.84	-0.01
BIO4.BIO5.BIO18.BIO19	0.86	0.82	-0.04	0.81	-0.05	-	-	-	-	-	-	0.84	-0.02	0.85	-0.01
BIO5.BIO15.BIO18.BIO19	0.84	-	-	*	-	-	-	-	-	0.82	-0.02	0.81	-0.03	0.82	-0.02
BIO6.BIO15.BIO18.BIO19	0.83	-	-	-	-	*	-	-	-	0.82	-0.01	-0.80	-0.03	-0.82	-0.01
Mean variable importance	**-**	**-**	**-0.040**	**-**	**-0.048**	**-**	**-**	**-**	**-0.030**	**-**	**-0.015**	**-**	**-0.026**	**-**	**-0.012**

Table 2.4: Variable importance for species at high latitudes (>23.5).

Combination	AUC	BIO4	AUC change	BIO5	AUC change	BIO6	AUC change	BIO12	AUC change	BIO15	AUC change	BIO18	AUC change	BIO19	AUC change
BIO4.BIO15.BIO18.BIO19	0.82	*	-	-	-	-	-	-	-	0.80	-0.02	0.79	-0.03	0.81	-0.01
BIO4.BIO5.BIO12.BIO15	0.87	0.83	-0.04	0.81	-0.06	-	-	0.85	-0.02	0.85	-0.02	-	-	-	-
BIO4.BIO5.BIO15.BIO18	0.86	0.83	-0.03	0.81	-0.05	-	-	-	-	0.85	-0.01	0.85	-0.01	-	-
BIO4.BIO5.BIO15.BIO19	0.86	0.82	-0.04	0.79	-0.07	-	-	-	-	0.84	-0.02	-	-	0.85	-0.01
BIO4.BIO5.BIO18.BIO19	0.86	0.83	-0.03	0.80	-0.06	-	-	-	-	-	-	0.84	-0.02	0.85	-0.01
BIO5.BIO15.BIO18.BIO19	0.84	-	-	*	-	-	-	-	-	0.83	-0.01	0.82	-0.02	0.83	-0.01
BIO6.BIO15.BIO18.BIO19	0.83	-	-	-	-	*	-	-	-	0.82	-0.01	0.80	-0.03	0.82	-0.01
Mean variable importance	**-**	**-**	**-0.035**	**-**	**-0.06**	**-**	**-**	**-**	**-0.02**	**-**	**-0.015**	**-**	**-0.022**	**-**	**-0.01**

Table 2.5: Variable importance for species at medium latitudes (<23.5 > -23.5, Tropics).

Combination	**AUC**	**BIO4**	**AUC change**	**BIO5**	**AUC change**	**BIO6**	**AUC change**	**BIO12**	**AUC change**	**BIO15**	**AUC change**	**BIO18**	**AUC change**	**BIO19**	**AUC change**
BIO4.BIO15.BIO18.BIO19	0.84	*	-	-	-	-	-	-	-	0.83	-0.01	0.82	-0.02	0.83	-0.01
BIO4.BIO5.BIO12.BIO15	0.86	0.81	-0.05	0.84	-0.02	-	-	0.83	-0.03	0.85	-0.01	-	-	-	-
BIO4.BIO5.BIO15.BIO18	0.85	0.81	-0.04	0.83	-0.02	-	-	-	-	0.84	-0.01	0.84	-0.01	-	-
BIO4.BIO5.BIO15.BIO19	0.85	0.79	-0.06	0.82	-0.03	-	-	-	-	0.83	-0.02	-	-	0.84	-0.01
BIO4.BIO5.BIO18.BIO19	0.85	0.80	-0.05	0.83	-0.02	-	-	-	-	-	-	0.83	-0.02	0.84	-0.01
BIO5.BIO15.BIO18.BIO19	0.82	-	-	*	-	-	-	-	-	-	-	0.79	-0.03	0.81	-0.01
BIO6.BIO15.BIO18.BIO19	0.84	-	-	-	-	*	-	-	-	0.82	-0.02	0.80	-0.04	0.83	-0.01
Mean variable importance	**-**	**-**	**-0.05**	**-**	**-0.023**	**-**	**-**	**-**	**-0.03**	**-**	**-0.014**	**-**	**-0.024**	**-**	**-0.01**

Table 2.6: Variable importance for species at low latitudes (< -23.5).

Combination	**AUC**	**BIO4**	**AUC change**	**BIO5**	**AUC change**	**BIO6**	**AUC change**	**BIO12**	**AUC change**	**BIO15**	**AUC change**	**BIO18**	**AUC change**	**BIO19**	**AUC change**
BIO4.BIO15.BIO18.BIO19	0.88	*	-	-	-	-	-	-	-	0.86	-0.02	0.85	-0.03	0.87	-0.01
BIO4.BIO5.BIO12.BIO15	0.88	0.85	-0.03	0.87	-0.01	-	-	0.88	0	0.86	-0.02	-	-	-	-
BIO4.BIO5.BIO15.BIO18	0.88	0.83	-0.05	0.87	-0.01	-	-	-	-	0.86	-0.02	0.88	0	-	-
BIO4.BIO5.BIO15.BIO19	0.87	0.81	-0.06	0.85	-0.02	-	-	-	-	0.86	-0.01	-	-	0.88	-0.01
BIO4.BIO5.BIO18.BIO19	0.87	0.83	-0.04	0.86	-0.01	-	-	-	-	-	-	0.86	-0.01	0.86	-0.01
BIO5.BIO15.BIO18.BIO19	0.84	-	-	*	-	-	-	-	-	0.83	-0.01	0.81	-0.03	0.83	-0.01
BIO6.BIO15.BIO18.BIO19	0.86	-	-	-	-	*	-	-	-	0.86	0	0.83	-0.03	0.85	-0.01
Mean variable importance	**-**	**-**	**-0.045**	**-**	**-0.0125**	**-**	**-**	**-**	**0**	**-**	**-0.013**	**-**	**-0.02**	**-**	**-0.01**

10. Supplementary material Chapter 3

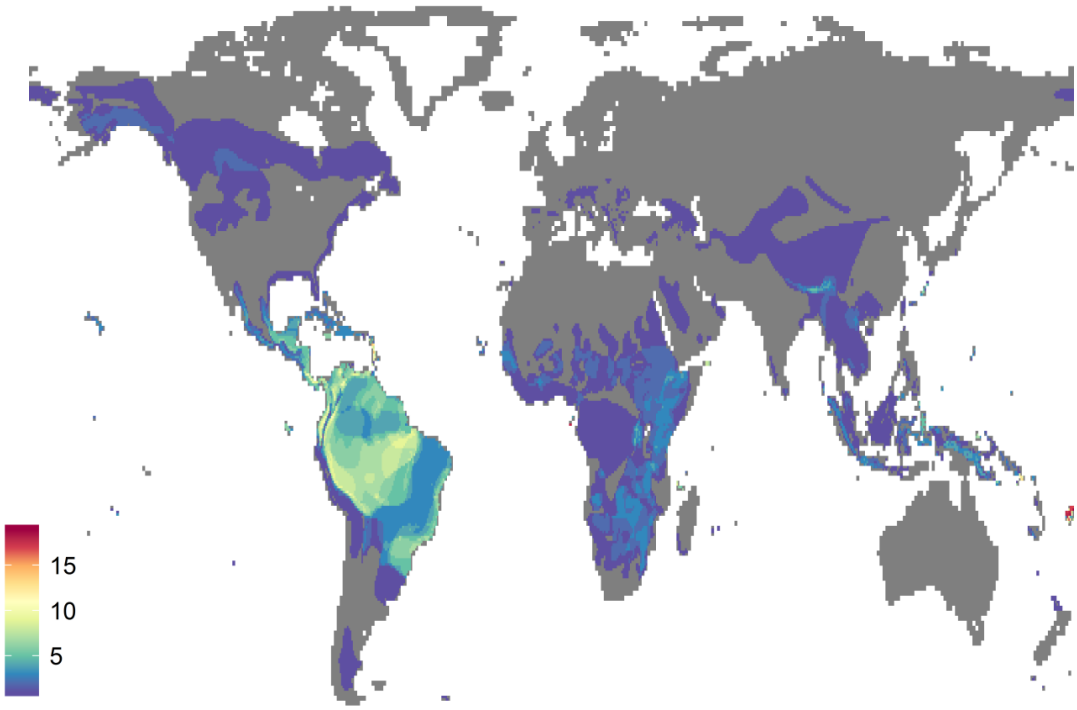

Figure S3.1: Current distribution of the terrestrial bird species I was not able to fit species distribution models for (n=746).

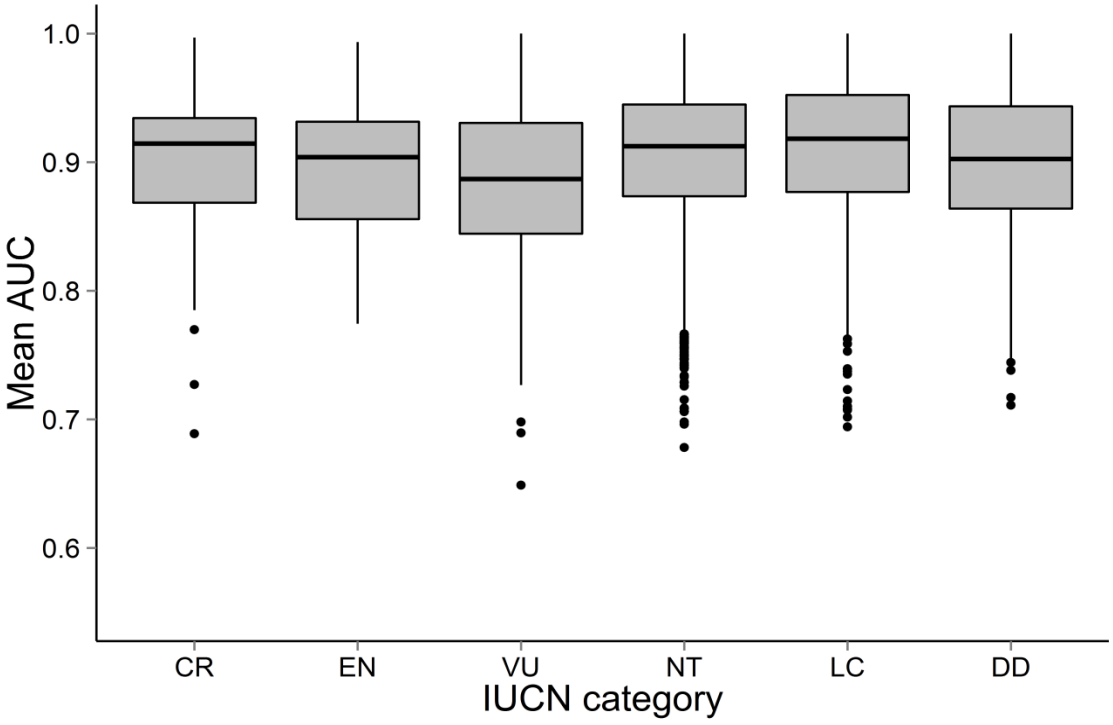

Figure S3.2: Mean AUC values for distribution models of species across the different IUCN categories.

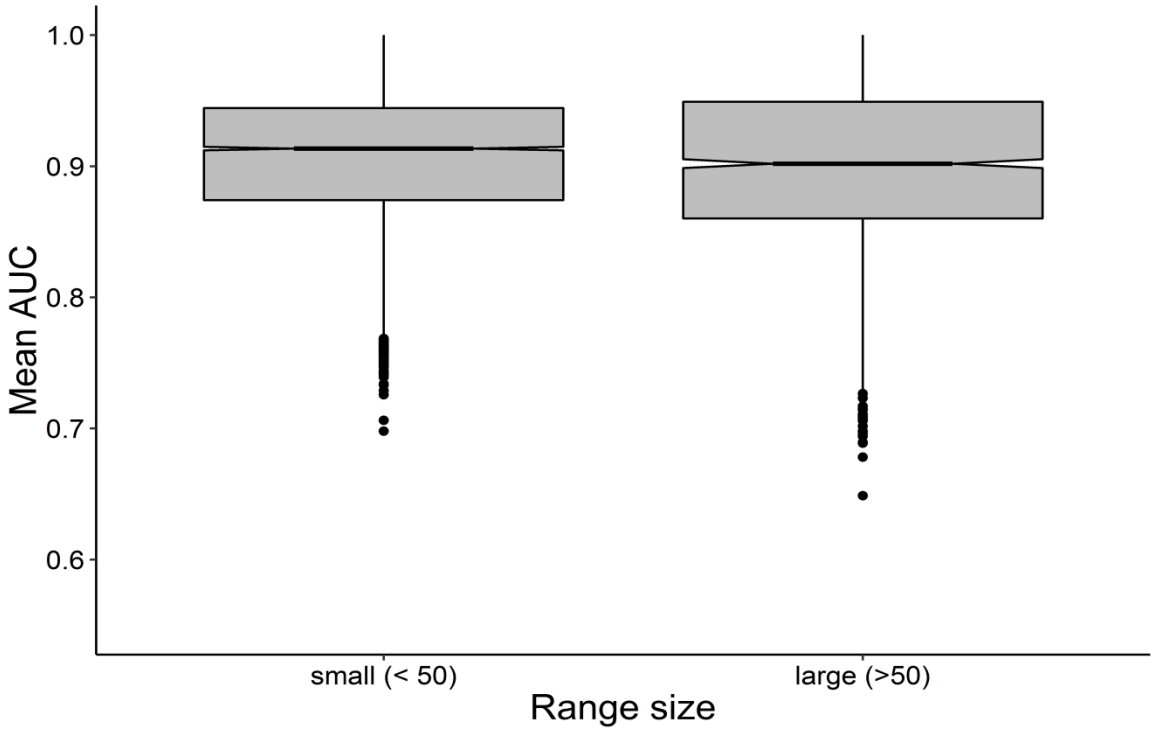

Figure S3.3: Mean AUC for species with a small range extent (<50 cells) and species with a large range (> 50 cells).

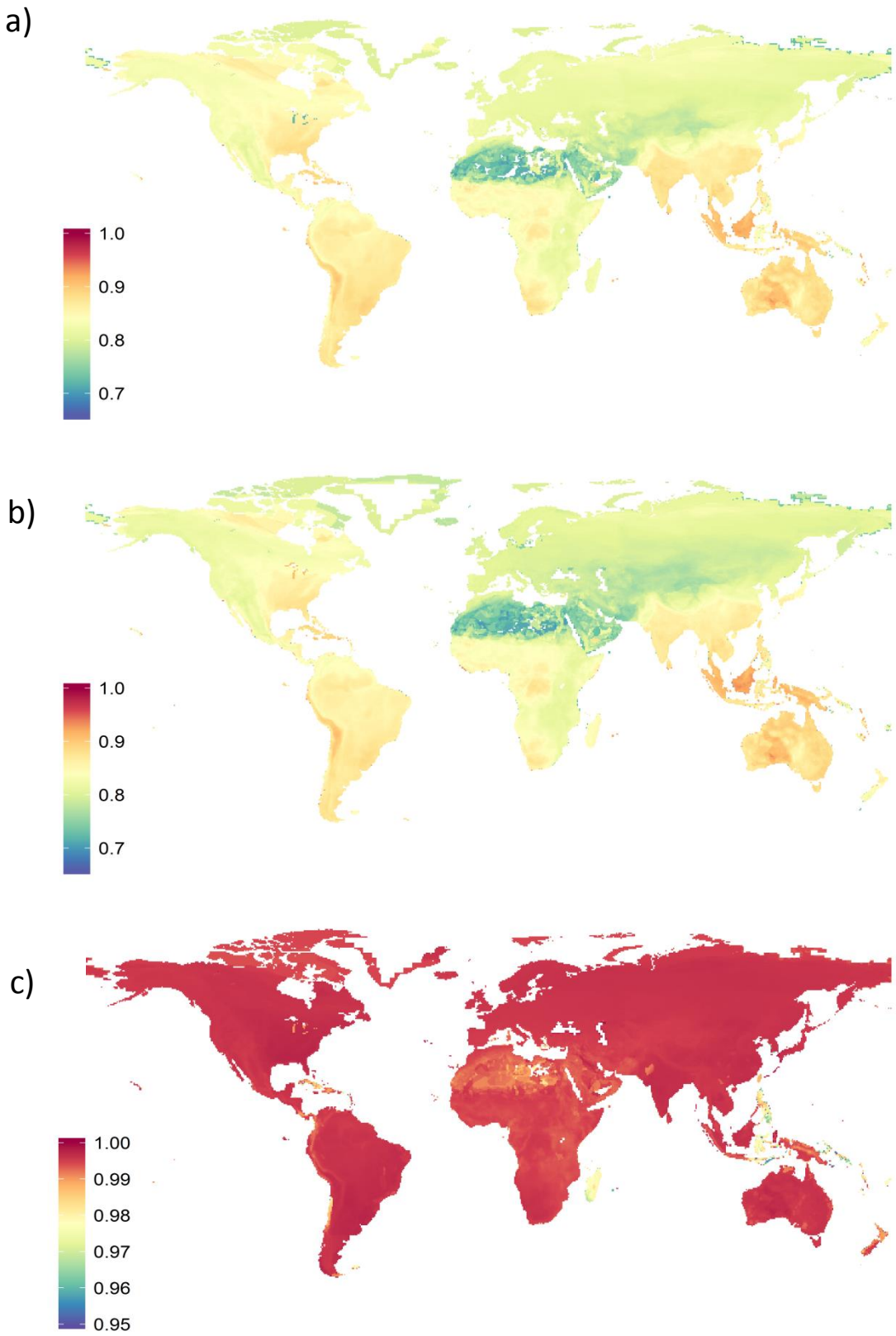

Figure S3.4: Mean AUC values across the models for all species occurring within a cell for the different model types; (a) General Additive Models, (b) Generalized Linear Models, (c) Random Forest Models.

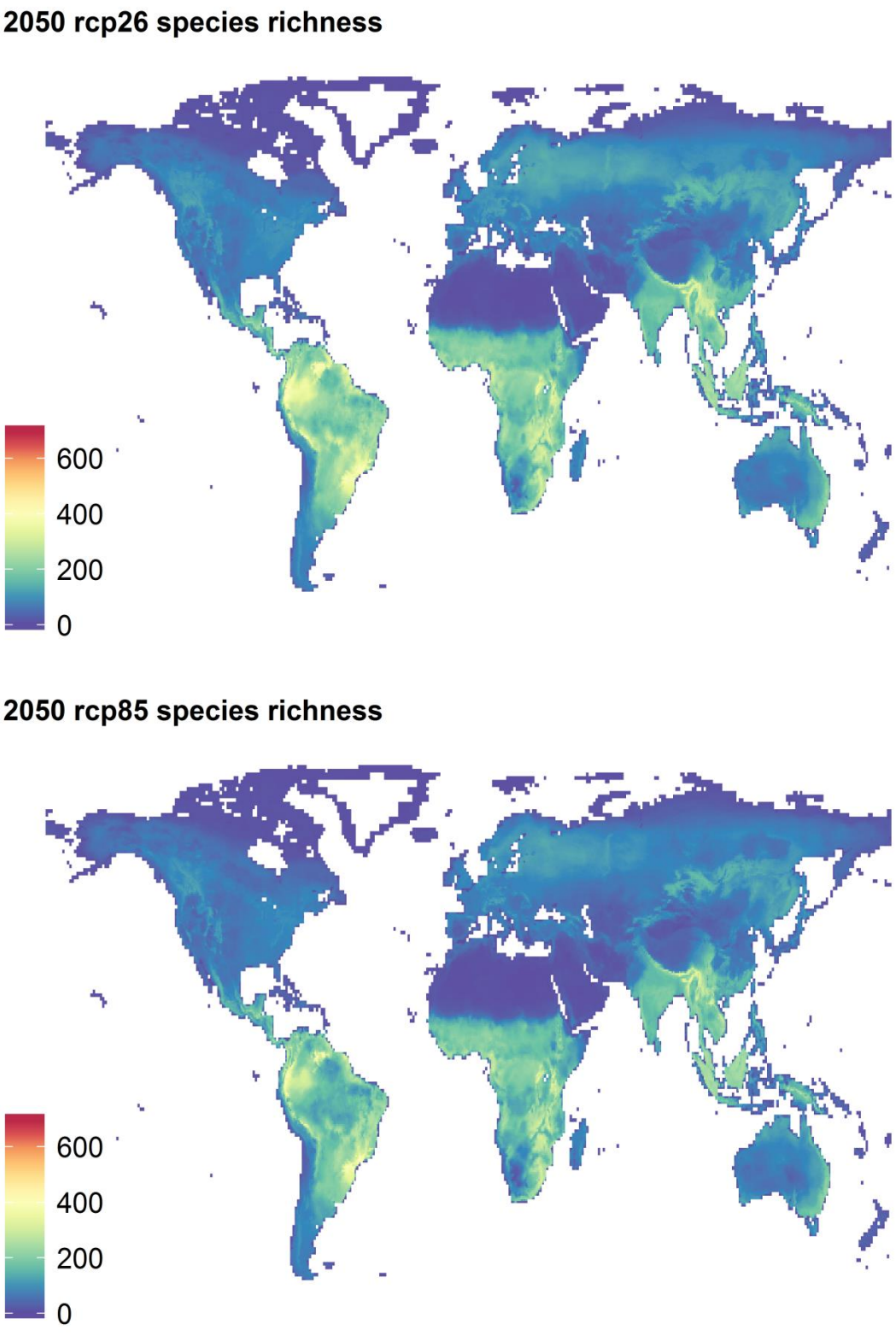

Figure S3.5: Predicted richness in 2050 based on an ensemble across SDMs and GCMs, under (a) emission scenario rcp26 and (b) emission scenario rcp85.

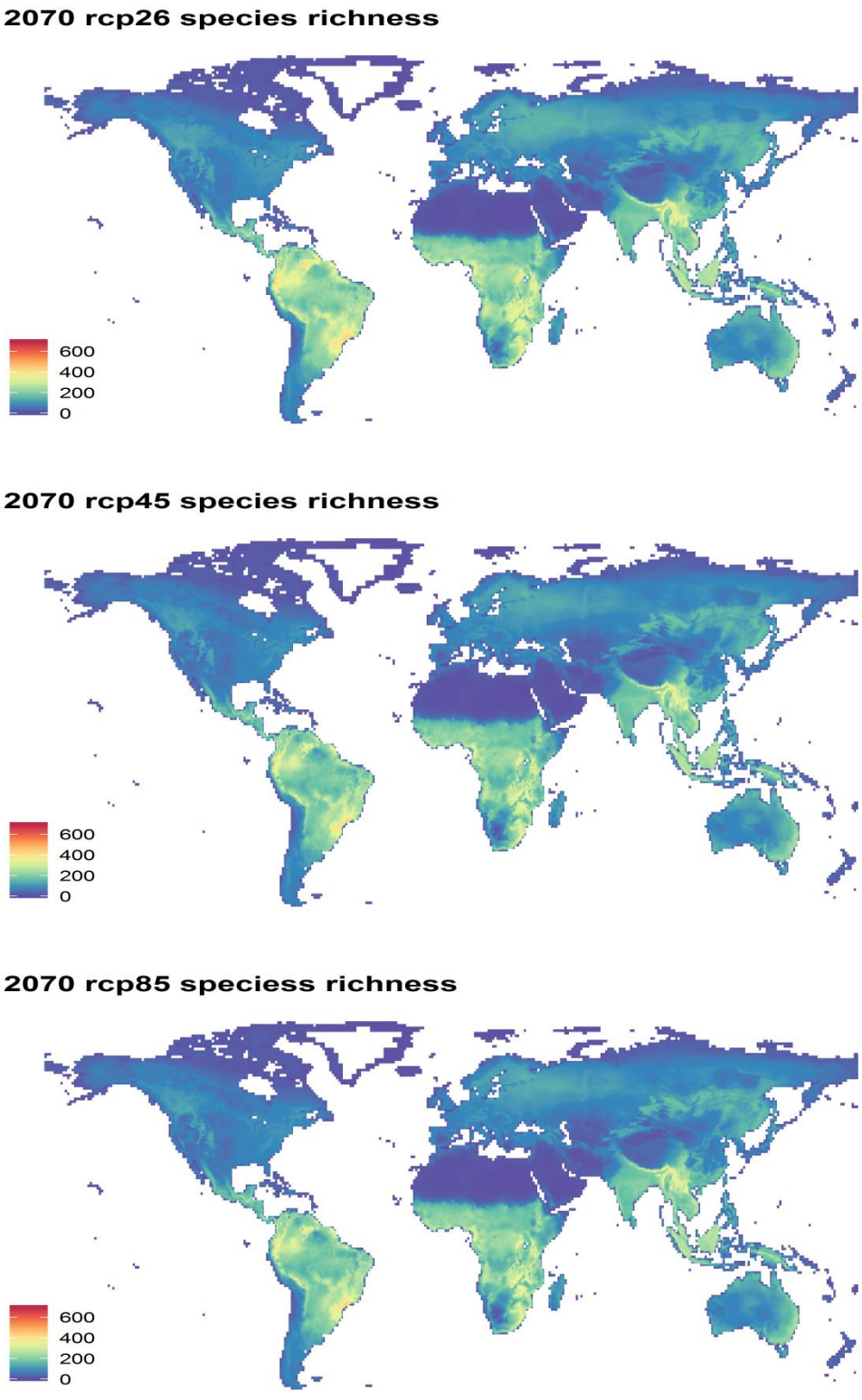

Figure S3.6: Predicted richness in 2050 based on an ensemble across SDMs and GCMs, under (a) emission scenario rcp26, (b) emission scenario rcp45 and (c) emission scenario rcp85.

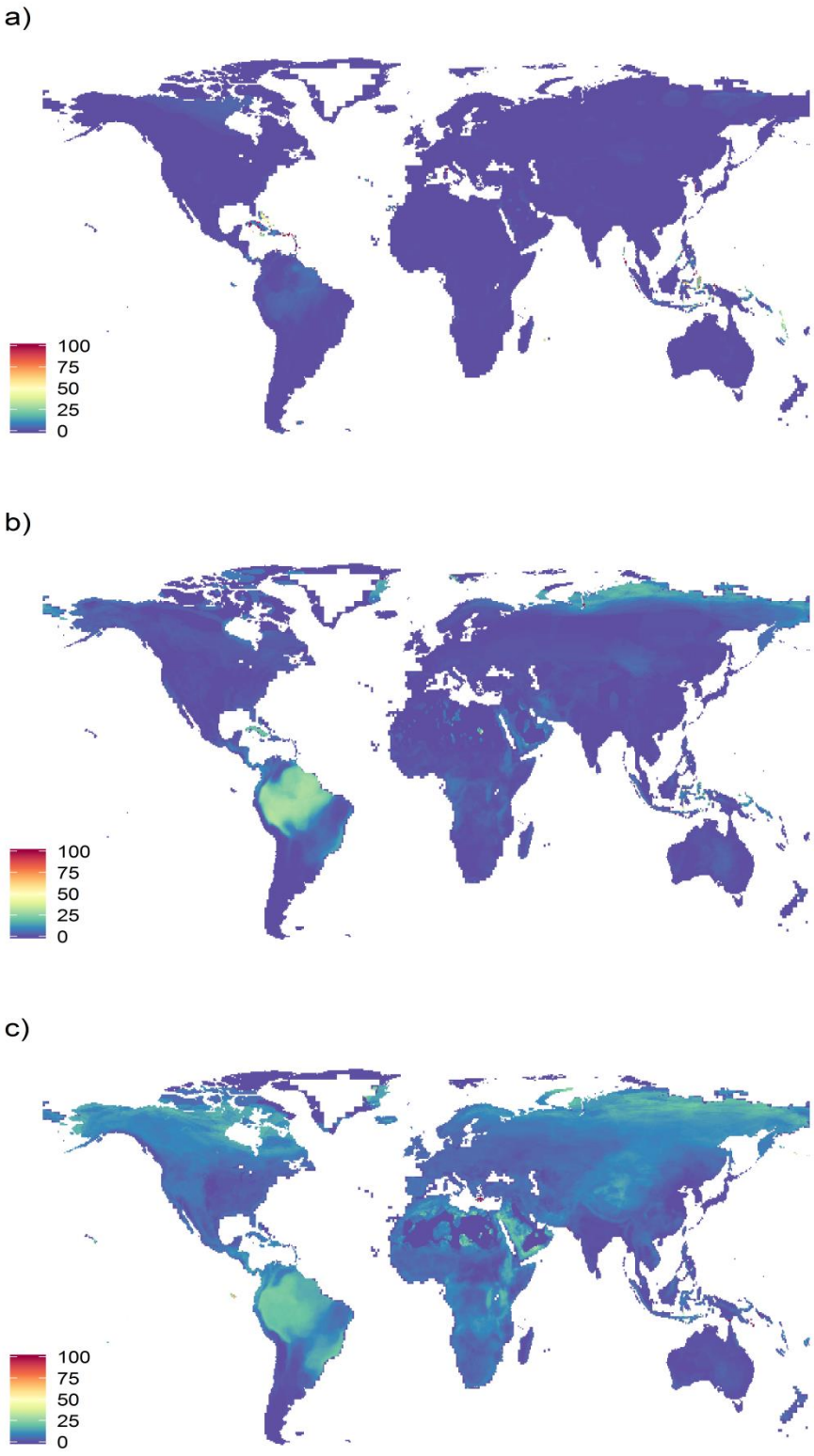

Figure S3.7: The proportion of species predicted to have the largest range declines under a medium emission scenario (rcp45) by 2050. (a) species predicted to be extinct by 2050, (b) species predicted to lose > 75% of their current range and (c) species predicted to lose between 50% and 75% of their current range extent.

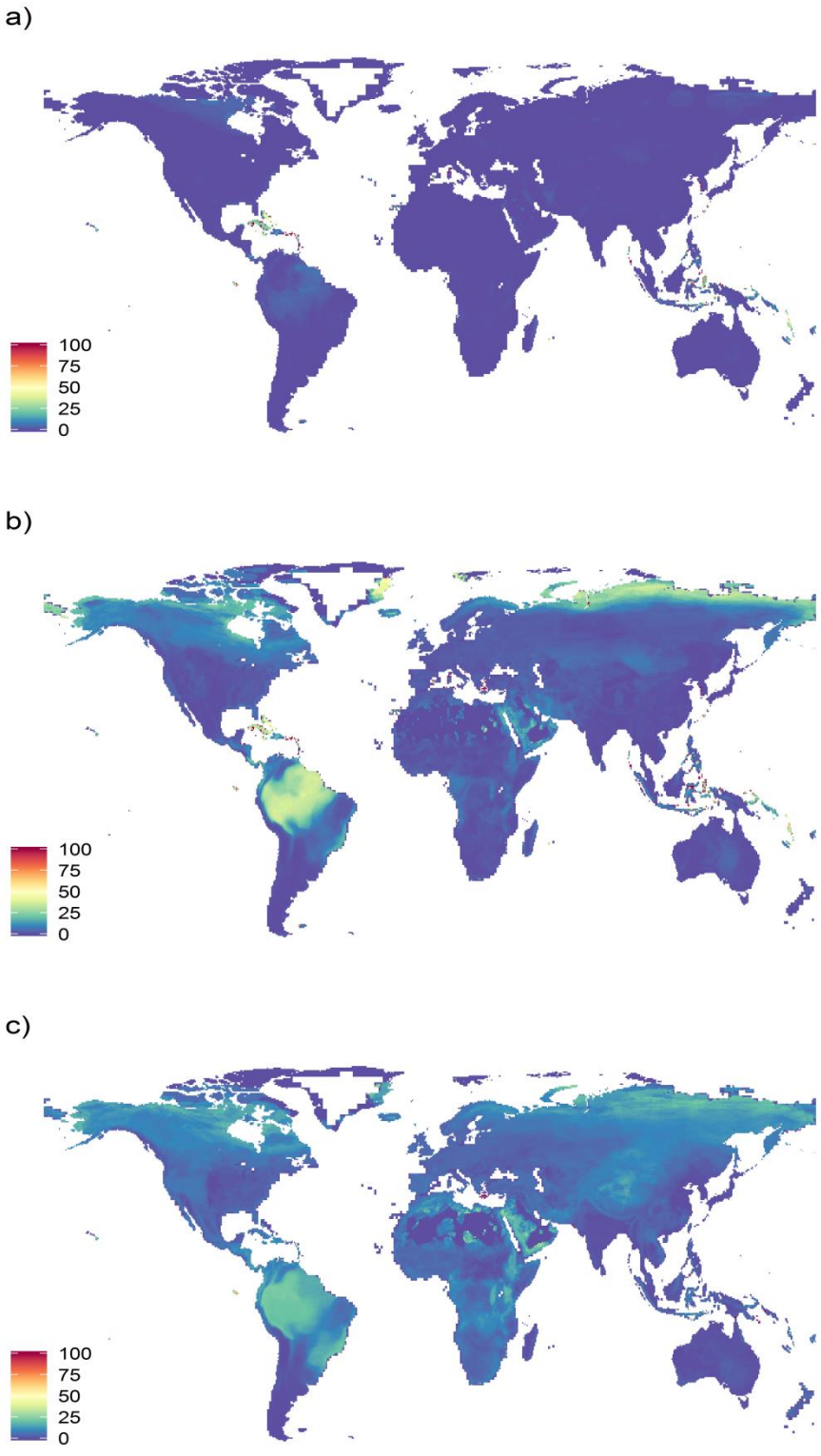

Figure S3.8: The proportion of species predicted to have the least overlap between their current and future range under a medium emission scenario (rcp45) by 2050. (a) species predicted to have no range overlap by 2050, (b) species predicted to have ≤ 25% overlap and (c) species that have < 50% and >25% overlap between their current and future range.

Table S3.1: Showing results for the Kruskal-Wallis post hoc test for pairwise comparisons, for the differences across latitudes. Significant values for differences between groups are highlighted in grey.

Proportional range change across latitude groups						
	-23 to -40	-40 to -60	>60	0 to -23	23 to 0	40 to 23
-40 to -60	3.6e-09	-	-	-	-	-
>60	0.0236	2.0e-12	-	-	-	-
0 to -23	4.9e-09	< 2e-16	0.9490	-	-	-
23 to 0	0.9953	4.1e-09	0.0052	< 2e-16	-	-
40 to 23	1.0000	7.0e-09	0.0177	8.8e-10	0.9994	-
60 to 40	0.8977	9.2e-07	0.0026	5.3e-12	0.9802	0.9453
Percentage overlap between current and future range across latitude groups						
	-23 to -40	-40 to -60	>60	0 to -23	23 to 0	40 to 23
-40 to -60	0.5957	-	-	-	-	-
>60	< 2e-16	8.9e-16	-	-	-	-
0 to -23	< 2e-16	1.0e-06	1.7e-07	-	-	-
23 to 0	0.0749	0.0426	3.8e-15	< 2e-16	-	-
40 to 23	0.6747	0.1389	4.2e-15	6.6e-10	0.9920	-
60 to 40	0.0169	0.0094	5.6e-11	0.0164	0.8218	0.6284
Distance between current and future range centre across latitude groups						
	-23 to -40	-40 to -60	>60	0 to -23	23 to 0	40 to 23
-40 to -60	0.99994	-	-	-	-	-
>60	< 2e-16	< 2e-16	-	-	-	-
0 to -23	0.33465	0.99883	< 2e-16	-	-	-
23 to 0	0.15721	0.84798	< 2e-16	1.5e-14	-	-
40 to 23	0.78712	0.99979	< 2e-16	0.99996	0.00011	-
60 to 40	< 2e-16	8.9e-16	0.00059	< 2e-16	< 2e-16	< 2e-16

Table S3.2: Showing results for the Kruskal-Wallis post hoc test for pairwise comparisons, for the differences across range sizes (numbers of cells occupied). Significant values for differences between groups are highlighted in grey.

Proportional range change across range groups				
	<1500	<2500	<50	<500
<2500	0.055	-	-	-
<50	1.5e-08	4.3e-13	-	-
<500	0.999	0.016	2.0e-11	-
>2500	< 2e-16	5.4e-06	< 2e-16	< 2e-16
Percentage overlap between current and future range across range groups				
	<1500	<2500	<50	<500
<2500	0.037	-	-	-
<50	< 2e-16	< 2e-16	-	-
<500	9.3e-05	8.1e-10	< 2e-16	-
>2500	< 2e-16	3.5e-06	< 2e-16	< 2e-16
Distance between current and future range centre across range groups				
	<1500	<2500	<50	<500
<2500	0.013			
<50	< 2e-16	< 2e-16		
<500	< 2e-16	< 2e-16	< 2e-16	
>2500	2.4e-06	0.690	< 2e-16	< 2e-16

Table S3.3: Showing results for the Kruskal-Wallis post hoc test for pairwise comparisons, for the differences across altitudes. Significant values for differences between groups are highlighted in grey.

Proportional range change across altitude groups				
	<1000	<1500	<2000	<500
<1500	0.62	-	-	-
<2000	8.7e-13	2.0e-07	-	-
<500	0.75	1.00	2.4e-08	-
>2000	< 2e-16	6.7e-16	0.60	< 2e-16
Percentage overlap between current and future range across altitude groups				
	<1000	<1500	<2000	<500
<1500	0.9998	-	-	-
<2000	2.5e-10	1.9e-08	-	-
<500	0.0101	0.0498	0.0038	-
>2000	6.7e-16	2.1e-12	0.9972	5.9e-05
Distance between current and future range centre across altitude groups				
	<1000	<1500	<2000	<500
<1500	0.92232	-	-	-
<2000	0.55328	0.23085	-	-
<500	0.42966	0.13561	0.99996	-
>2000	0.00036	0.03001	2.0e-05	3.3e-07

11. Supplementary material Chapter 4

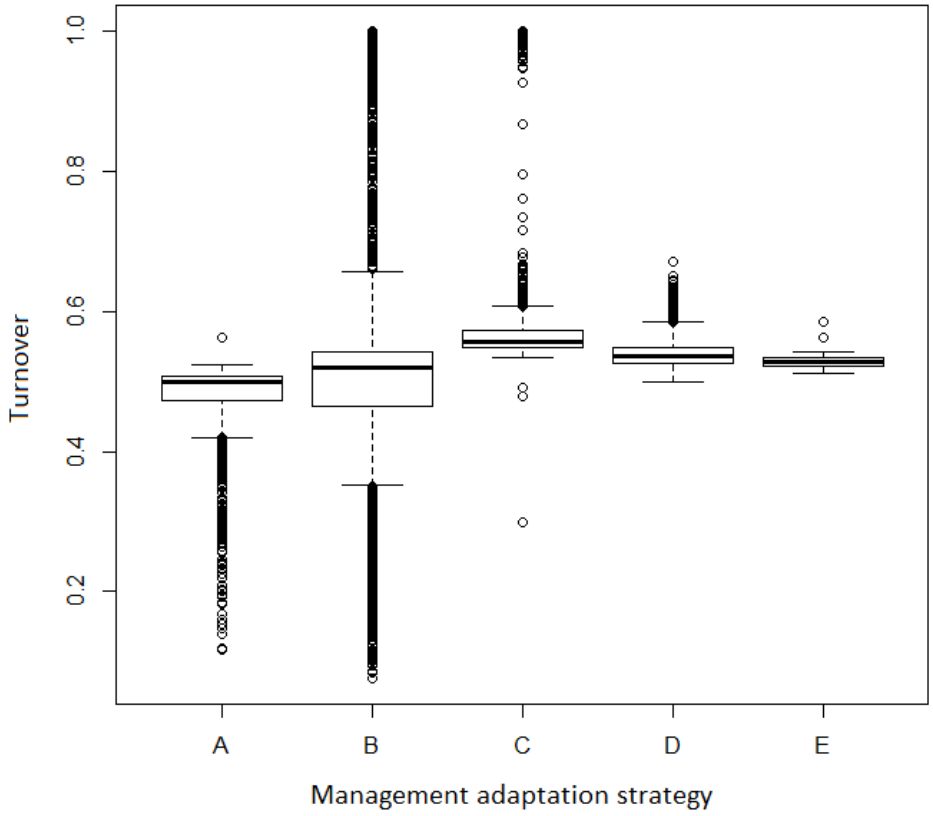

Figure S4.1: Medium turnover per Important Bird Area (IBA) for each of the management adaptation strategies, high persistence (A), increasing value (B), high turnover (C), increasing specification (D) and increasing diversification (D).

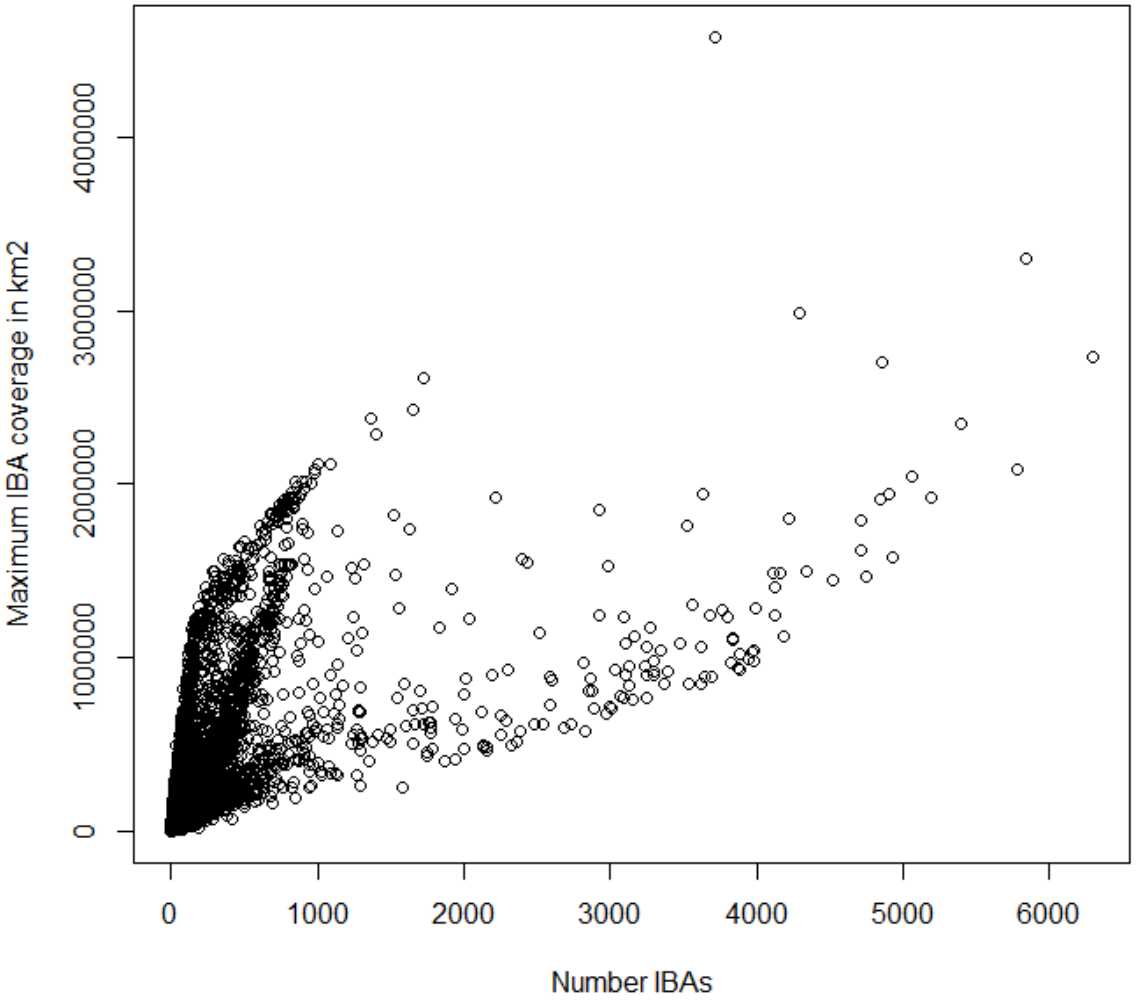

Figure S4.2: The maximum amount of km^2 of Important Bird Area (IBA) a species is currently covered by plotted against the number of IBAs a species occurs in.

12. Supplementary material Chapter 5

Table S5.1: The associations used to match IUCN level one habitat classifications with the ESA Global Land Cover data (slightly modified from Butchart et al. unpublished work, 2016).

BirdLife (IUCN level one habitat classification)	**GlobCover ID(s)**	**GlobCover description**
Artificial/Aquatic - Aquaculture Ponds	210	Water bodies
Artificial/Aquatic - Canals and Drainage Channels, Ditches	210	Water bodies
Artificial/Aquatic - Excavations (open)	211	Water bodies
Artificial/Aquatic - Irrigated Land (includes irrigation channels)	20	Cropland, irrigated or post-flooding
Artificial/Aquatic - Ponds (below 8ha)	210	Water bodies
Artificial/Aquatic - Salt Exploitation Sites	211	Water bodies
Artificial/Aquatic - Seasonally Flooded Agricultural Land	20	Cropland, irrigated or post-flooding
Artificial/Aquatic - Wastewater Treatment Areas	210	Water bodies
Artificial/Aquatic - Water Storage Areas (over 8ha)	210	Water bodies
Artificial/Terrestrial - Arable Land	30 10	Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%) / Cropland, rainfed
Artificial/Terrestrial - Pastureland	30 10	Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%) Cropland, rainfed
Artificial/Terrestrial - Plantations	30	Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%)
Artificial/Terrestrial - Rural Gardens	30	Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%)
Artificial/Terrestrial - Subtropical/Tropical Heavily Degraded Former Forest	30	Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%)
Artificial/Terrestrial - Urban Areas	190	Urban areas
Caves and Subterranean Habitats (non-aquatic) - Caves	0	No Data
Caves and Subterranean Habitats (non-aquatic) - Other Subterranean Habitats	0	No Data

Desert - Hot	200 202	Bare areas / Unconsolidated bare areas
Desert - Temperate	200 202	Bare areas / Unconsolidated bare areas
Desert - Cold	200 202	Bare areas / Unconsolidated bare areas
Forest - Boreal	70 71 72	Tree cover, needle leaved, evergreen, closed to open (>15%) / Tree cover, needle leaved, evergreen, closed (>40%) / Tree cover, needle leaved, evergreen, open (15-40%)
Forest - Sub Antarctic	90	Tree cover, mixed leaf type (broadleaved and needle leaved)
Forest - Subarctic	80 81 82	Tree cover, needle leaved, deciduous, closed to open (>15%) /deciduous, closed to open (>15%) 81 Tree cover, needle leaved, deciduous, closed (>40%) / Tree cover, needle leaved, deciduous, open (15-40%)
Forest - Subtropical/Tropical Dry	61	Tree cover, broadleaved, deciduous, closed (>40%)
Forest - Subtropical/Tropical Mangrove Vegetation Above High Tide Level	170	Tree cover, flooded, saline water
Forest - Subtropical/Tropical Moist Lowland	50	Tree cover, broadleaved, evergreen, closed to open (>15%)
Forest - Subtropical/Tropical Moist Montane	50	Tree cover, broadleaved, evergreen, closed to open (>15%)
Forest - Subtropical/Tropical Swamp	160	Tree cover, flooded, fresh or brackish water
Forest - Temperate	160	Tree cover, flooded, fresh or brackish water
Grassland - Subantarctic	11 153 130	Herbaceous cover / Sparse herbaceous cover (<15%) / Grassland
Grassland - Subarctic	11 153 130	Herbaceous cover / Sparse herbaceous cover (<15%) / Grassland
Grassland - Subtropical/Tropical Dry	11 153 130	Herbaceous cover / Sparse herbaceous cover (<15%) / Grassland
Grassland - Subtropical/Tropical High Altitude	11 153 130	Herbaceous cover / Sparse herbaceous cover (<15%) / Grassland
Grassland - Subtropical/Tropical Seasonally Wet/Flooded	11 153 180 130	Herbaceous cover / Sparse herbaceous cover (<15%) / Shrub or herbaceous cover, flooded, fresh/saline/brackish water / Grassland
Grassland - Temperate	11 153 130	Herbaceous cover / Sparse herbaceous cover (<15%) / Grassland
Grassland - Tundra	11 153 130	Herbaceous cover / Sparse herbaceous cover (<15%) / Grassland
Introduced vegetation	11 153 30 40	Herbaceous cover / Sparse herbaceous cover (<15%) / Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%) / Mosaic natural vegetation (tree, shrub, herbaceous cover) (>50%) / cropland (<50%)
Marine Coastal/Supratidal - Coastal Brackish/Saline Lagoons/Marine Lakes	160 170 180	Tree cover, flooded, fresh or brackish water / Tree cover, flooded, saline water / Shrub or herbaceous cover, flooded, fresh/saline/brackish water

Marine Coastal/Supratidal - Coastal Freshwater Lakes	210	Water bodies
Marine Coastal/Supratidal - Coastal Sand Dunes	202	Unconsolidated bare areas
Marine Coastal/Supratidal - Sea Cliffs and Rocky Offshore Islands	201	Consolidated bare areas
Marine Intertidal - Mud Flats and Salt Flats	202 180	Unconsolidated bare areas / Shrub or herbaceous cover, flooded, fresh/saline/brackish water
Marine Intertidal - Rocky Shoreline	201	Consolidated bare areas
Marine Intertidal - Salt Marshes (Emergent Grasses)	202 180	Unconsolidated bare areas / Shrub or herbaceous cover, flooded, fresh/saline/brackish water
Marine Intertidal - Salt Marshes (Emergent Grasses)	210 180	Water bodies / Shrub or herbaceous cover, flooded, fresh/saline/brackish water
Marine Intertidal - Sandy Shoreline and/or Beaches, Sand Bars, Spits, Etc	200 202	Bare areas / Unconsolidated bare areas
Marine Intertidal - Shingle and/or Pebble Shoreline and/or Beaches	200 201	Bare areas / Consolidated bare areas
Marine Intertidal - Tide pools	210	Water bodies
Marine Neritic - Estuaries	0	No Data
Marine Neritic - Pelagic	0	No Data
Marine Oceanic - Epipelagic (0-200m)	0	No Data
Marine Oceanic - Mesopelagic (200-1000m)	0	No Data
Rocky areas (eg. inland cliffs, mountain peaks)	200 201	Bare areas / Consolidated bare areas
Savanna - Dry	120 122 150 152	Shrubland / Deciduous shrubland / Sparse vegetation (tree, shrub, herbaceous cover) (<15%) / Sparse shrub (<15%)
Savanna - Moist	120 122 150 152	Shrubland / Deciduous shrubland / Sparse vegetation (tree, shrub, herbaceous cover) (<15%) / Sparse shrub (<15%)
Shrubland - Boreal	120 121 122 150 152 12	Shrubland / Evergreen shrubland / Deciduous shrubland / Sparse vegetation (tree, shrub, herbaceous cover) (<15%) / Sparse shrub (<15%) /Tree or shrub cover
Shrubland - Mediterranean-type Shrubby Vegetation	120 121 122 150 152 12	Shrubland / Evergreen shrubland / Deciduous shrubland / Sparse vegetation (tree, shrub, herbaceous cover) (<15%) / Sparse shrub (<15%) /Tree or shrub cover
Shrubland - Sub Antarctic	120 121 122 150 152 12	Shrubland / Evergreen shrubland / Deciduous shrubland / Sparse vegetation (tree, shrub, herbaceous cover) (<15%) / Sparse shrub (<15%) /Tree or shrub cover

Shrubland - Subarctic	120 121 122 150 152 12	Shrubland / Evergreen shrubland / Deciduous shrubland / Sparse vegetation (tree, shrub, herbaceous cover) (<15%) / Sparse shrub (<15%) /Tree or shrub cover
Shrubland - Subtropical/Tropical Dry	120 121 122 150 152 12	Shrubland / Evergreen shrubland / Deciduous shrubland / Sparse vegetation (tree, shrub, herbaceous cover) (<15%) / Sparse shrub (<15%) /Tree or shrub cover
Shrubland - Subtropical/Tropical High Altitude	120 121 122 150 152 12	Shrubland / Evergreen shrubland / Deciduous shrubland / Sparse vegetation (tree, shrub, herbaceous cover) (<15%) / Sparse shrub (<15%) /Tree or shrub cover
Shrubland - Subtropical/Tropical Moist	120 121 122 150 152 180 12	Shrubland / Evergreen shrubland / Deciduous shrubland / Sparse vegetation (tree, shrub, herbaceous cover) (<15%) / Sparse shrub (<15%) / Shrub or herbaceous cover, flooded, fresh/saline/brackish water Tree or shrub cover
Shrubland - Temperate	120 121 122 150 152 180 12	Shrubland / Evergreen shrubland / Deciduous shrubland / Sparse vegetation (tree, shrub, herbaceous cover) (<15%) / Sparse shrub (<15%) / Shrub or herbaceous cover, flooded, fresh/saline/brackish water Tree or shrub cover
Wetlands (inland) - Alpine Wetlands (includes temporary waters from snowmelt)	210 180	Water bodies /Shrub or herbaceous cover, flooded, fresh/saline/brackish water
Wetlands (inland) - Alpine Wetlands (includes temporary waters from snowmelt)	210 180	Water bodies / Shrub or herbaceous cover, flooded, fresh/saline/brackish water
Wetlands (inland) - Bogs, Marshes, Swamps, Fens, Peatlands	210 180	Water bodies /Shrub or herbaceous cover, flooded, fresh/saline/brackish water
Wetlands (inland) - Freshwater Springs and Oases	210	Water bodies
Wetlands (inland) - Permanent Freshwater Lakes (over 8ha)	210	Water bodies
Wetlands (inland) - Permanent Freshwater Marshes/Pools (under 8ha)	180	Shrub or herbaceous cover, flooded, fresh/saline/brackish water
Wetlands (inland) - Permanent Inland Deltas	210 160 180	Water bodies / Tree cover, flooded, fresh or brackish water / Shrub or herbaceous cover, flooded, fresh/saline/brackish water
Wetlands (inland) - Permanent Rivers/Streams/Creeks (includes waterfalls)	210	Water bodies
Wetlands (inland) - Permanent Saline, Brackish or Alkaline Lakes	210	Water bodies
Wetlands (inland) - Permanent Saline, Brackish or Alkaline Marshes/Pools	210	Water bodies
Wetlands (inland) - Seasonal/Intermittent	210 160 180	Water bodies / Tree cover, flooded, fresh or brackish water / Shrub or herbaceous

Freshwater Lakes (over 8ha)		cover, flooded, fresh/saline/brackish water
Wetlands (inland) - Seasonal/Intermittent Freshwater Marshes/Pools (under 8ha)	210 160 180	Water bodies / Tree cover, flooded, fresh or brackish water / Shrub or herbaceous cover, flooded, fresh/saline/brackish water
Wetlands (inland) - Seasonal/Intermittent Saline, Brackish or Alkaline Lakes and Flats	210 160 180	Water bodies / Tree cover, flooded, saline water/ Shrub or herbaceous cover, flooded, fresh/saline/brackish water
Wetlands (inland) - Seasonal/Intermittent Saline, Brackish or Alkaline Marshes/Pools	210 160 180	Water bodies / Tree cover, flooded, saline water/ Shrub or herbaceous cover, flooded, fresh/saline/brackish water
Wetlands (inland) -Seasonal/Intermittent/Irregular Rivers/Streams/Creeks	210	Water bodies
Wetlands (inland) - Shrub Dominated Wetlands	210 180	Water bodies / Shrub or herbaceous cover, flooded, fresh/saline/brackish water
Wetlands (inland) - Tundra Wetlands (incl. pools and temporary waters from snowmelt)	211 180	Water bodies / Shrub or herbaceous cover, flooded, fresh/saline/brackish water
Wetlands (inland) - Geothermal Wetlands	210	Water bodies

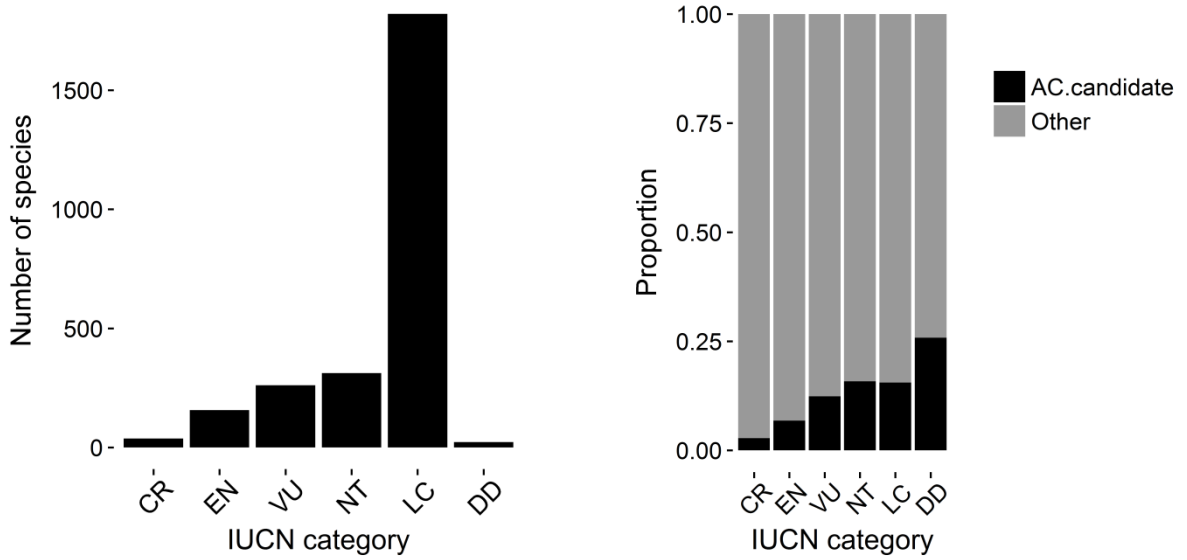

Figure S5.1: Distribution of the species selected as potential assisted colonisation candidates across the IUCN threat categories. Left graph shows the potential assisted colonisation candidates by 2070, right graph shows the proportion of assisted colonisation candidates within each category.

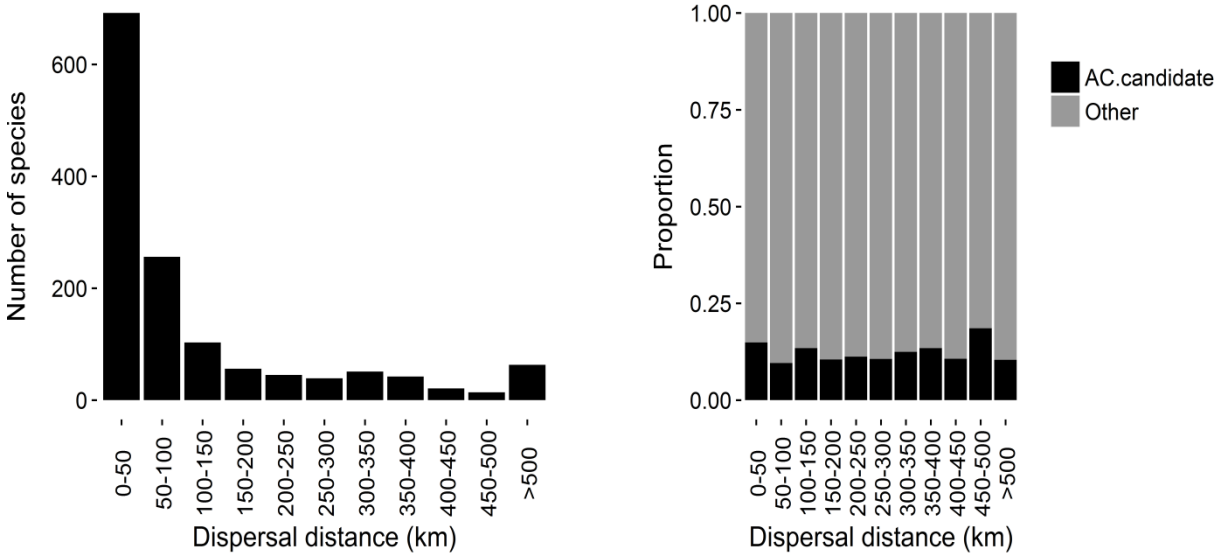

Figure S5.2: The number of species with differing dispersal capabilities that are considered AC candidates by (a) 2070 and (b) the proportion of AC candidate species across different dispersal distances

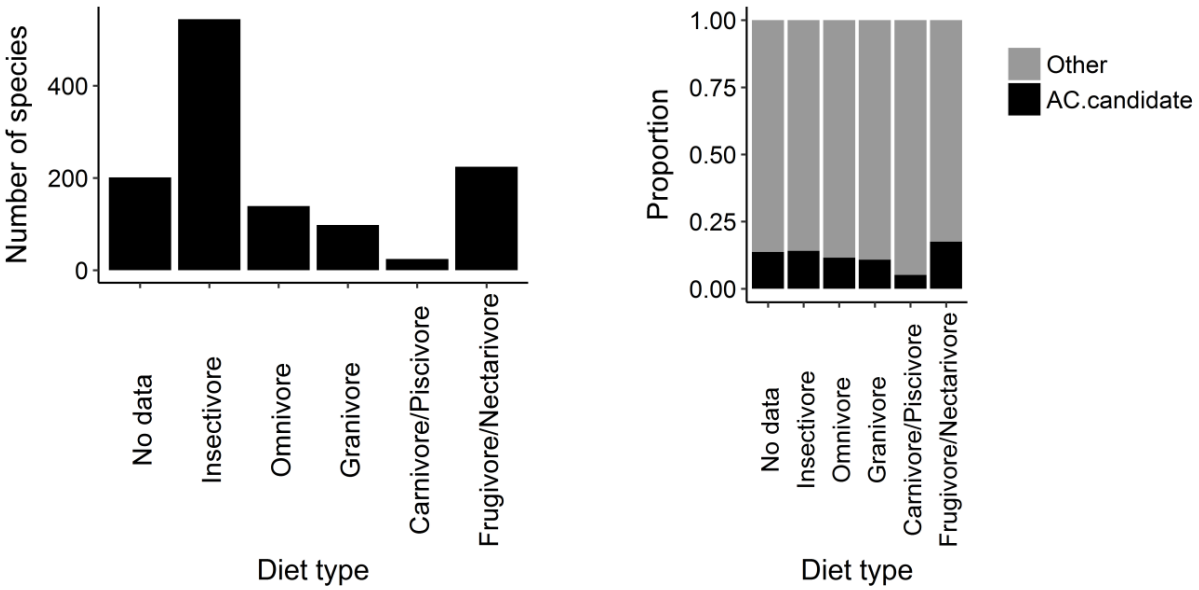

Figure S5.3: The number of species belonging to different feeding guilds that are considered AC candidates by (a) 2070 and (b) the proportion of AC candidate species across the different feeding guilds.

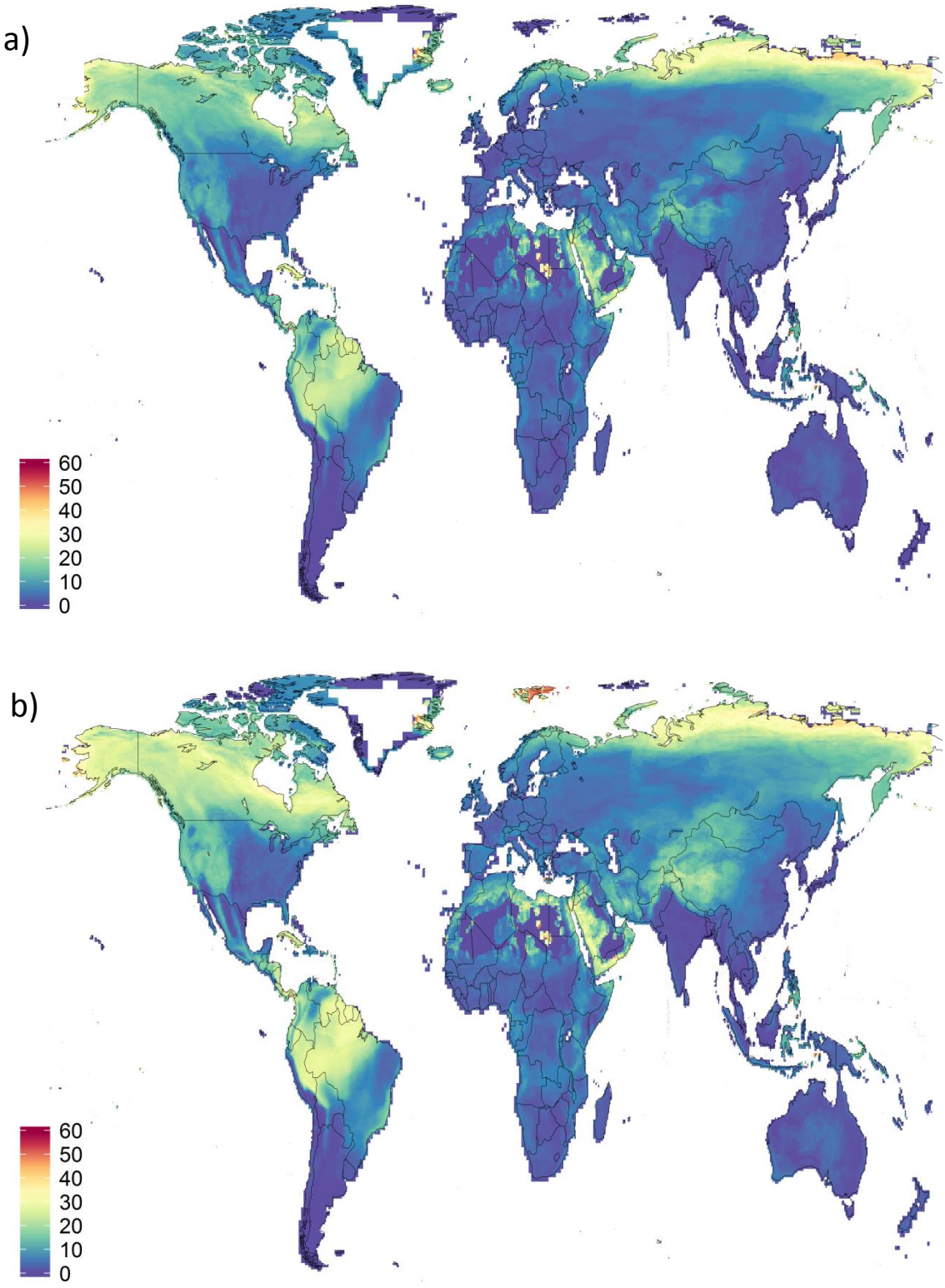

Figure S5.4: Proportion of AC candidates per grid cell by (a) 2050 and (b) 2070, based on the rcp45 emission scenario. Plots are based on ensemble median projections from the three SDMs and proportion values plotted are means across three GCMs.

12. Supplementary material Chapter 6

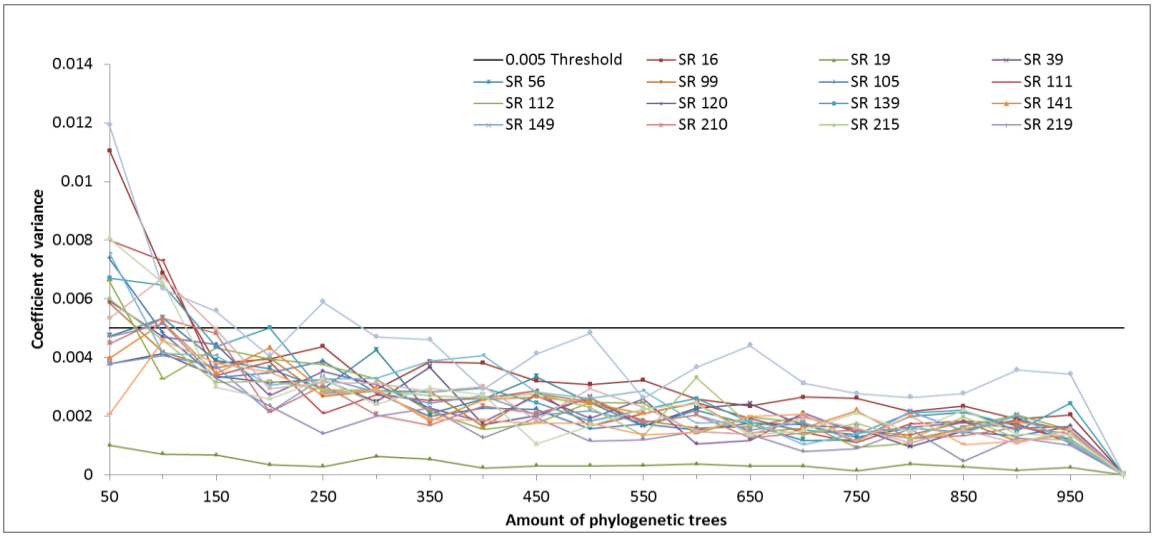

Figure S6.1*:* The coefficient of variation (for 20 randomly chosen grid cells) for PD plotted against the number of trees used to calculate PD. The black line indicates the coefficient of variation threshold of 0.005. Coloured lines and points represent data for individual cells. Cells had a SR between 16 and 219 species.

S6.1 Pilot study: Using a subset of the 10,000 available trees to estimate PD per cell

Due to computational limitations I used of a subset of the 10,000 available trees. To determine how many trees were necessary to produce a stable estimate of PD for a cell I undertook a pilot analysis on 20 randomly chosen cells from across the world. The species richness for these cells varied between 16 and 387 species per cell. I calculated PD values for each cell, using a random subset of 1000 trees (Rubolini *et al.*, 2015) out of the 10,000 phylogenetic trees from Jetz et al. (2012). I then calculated the change in the coefficient of variance of PD values per cell as more trees were added. I determined that using 200 of 1000 trees resulted in a coefficient of variance below 0.005 for 90% of the cells, i.e. the precision in PD increased to only a small extent if more than 200 trees were considered. Therefore, I subsequently calculated mean PD for all cells using 200 randomly chosen trees from the 10,000 available trees (Figure S6.1).

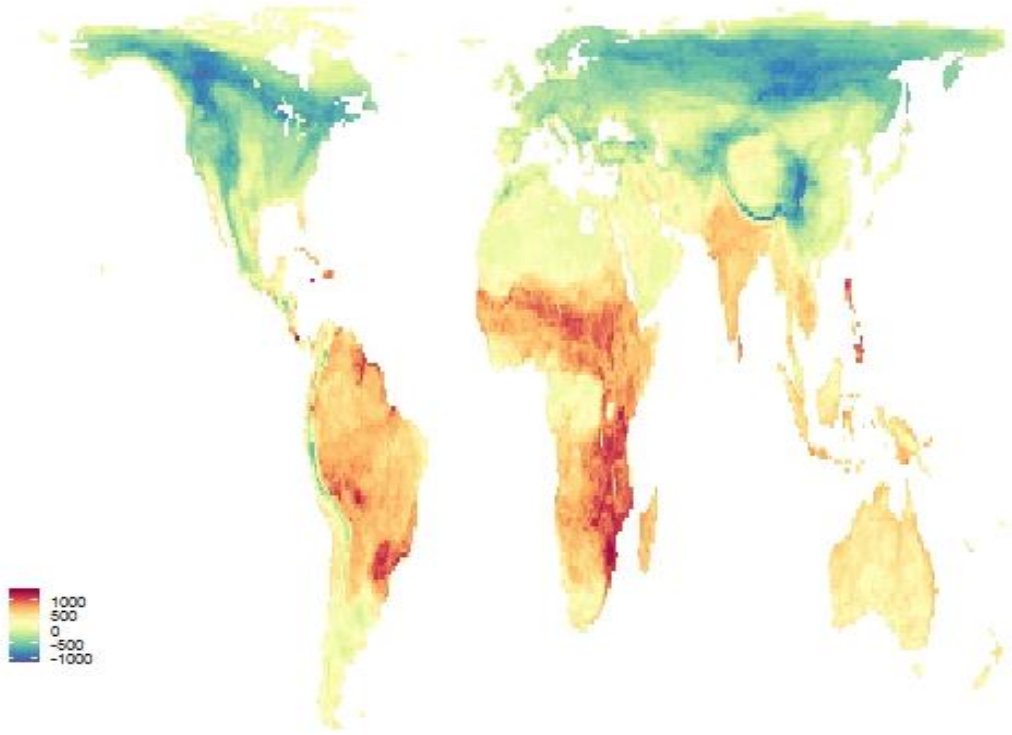

Figure S6.2: The residuals of the generalized (Michaelis- Menten) saturating curve. Red indicating areas of unusually high PD given the SR and blue indicating unusually low PD given the SR.

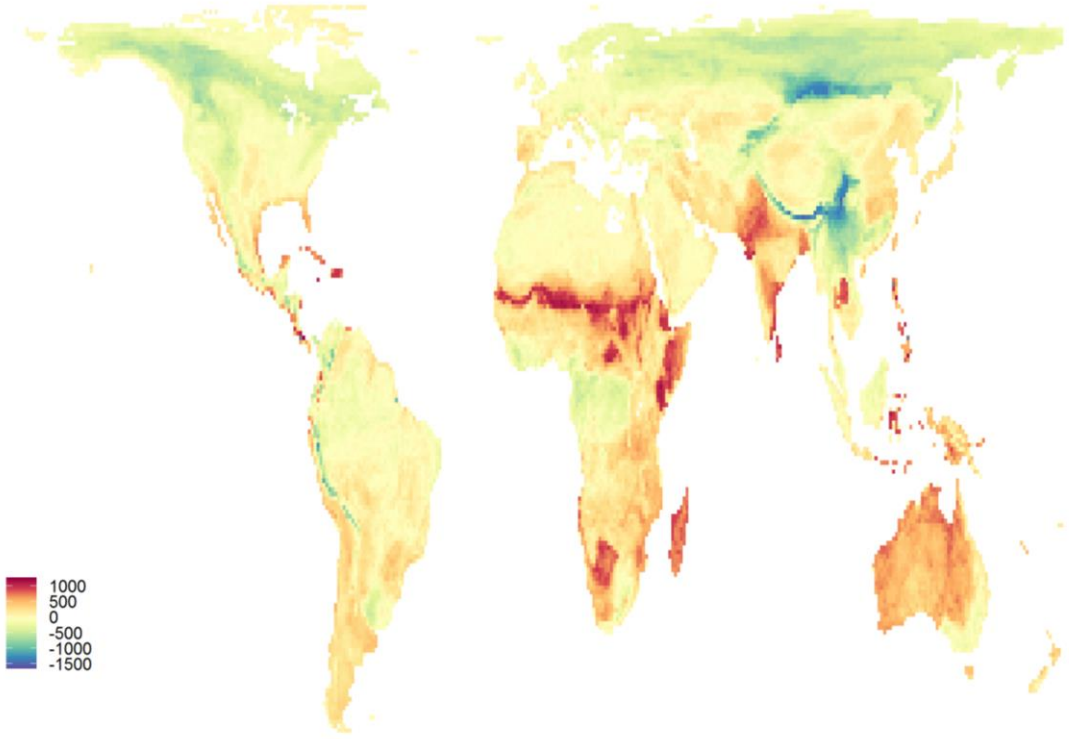

Figure S6.3: The residuals of the LOESS regression. Red indicating areas of unusually high PD given the SR and blue indicating unusually low PD given the SR.

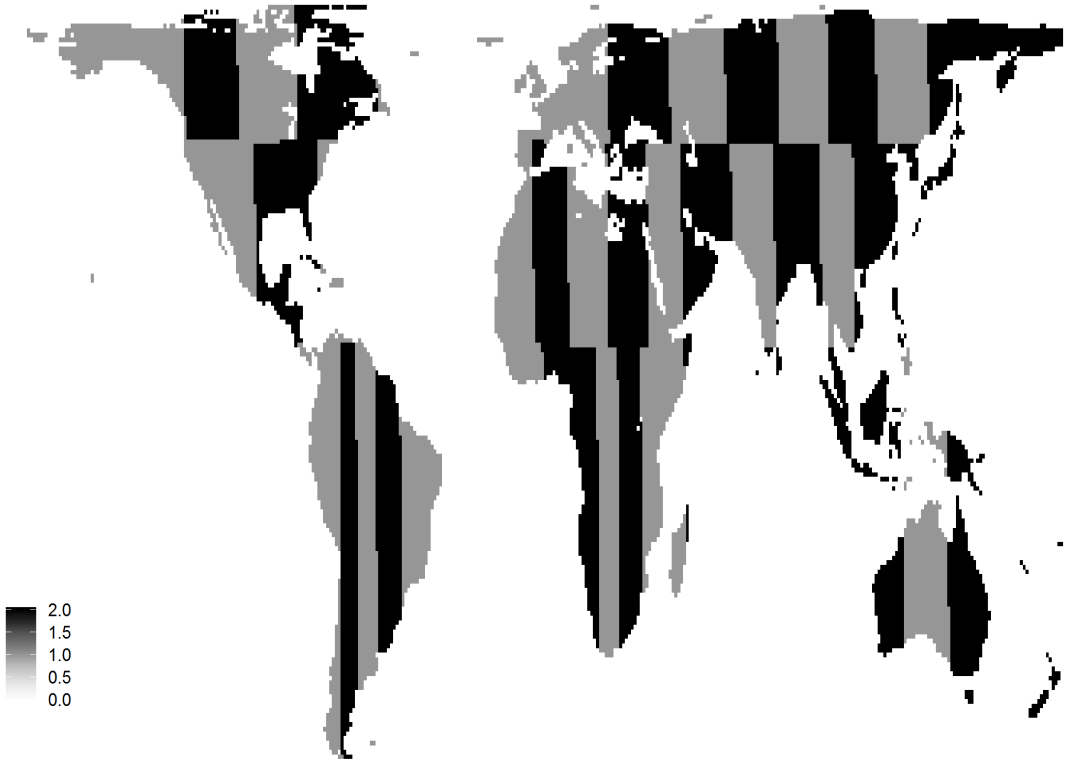

Figure S6.4: The 36 blocks across three latitudinal bands used for data subsampling – see methods. The blocks were divided in two groups using a checkerboard pattern.

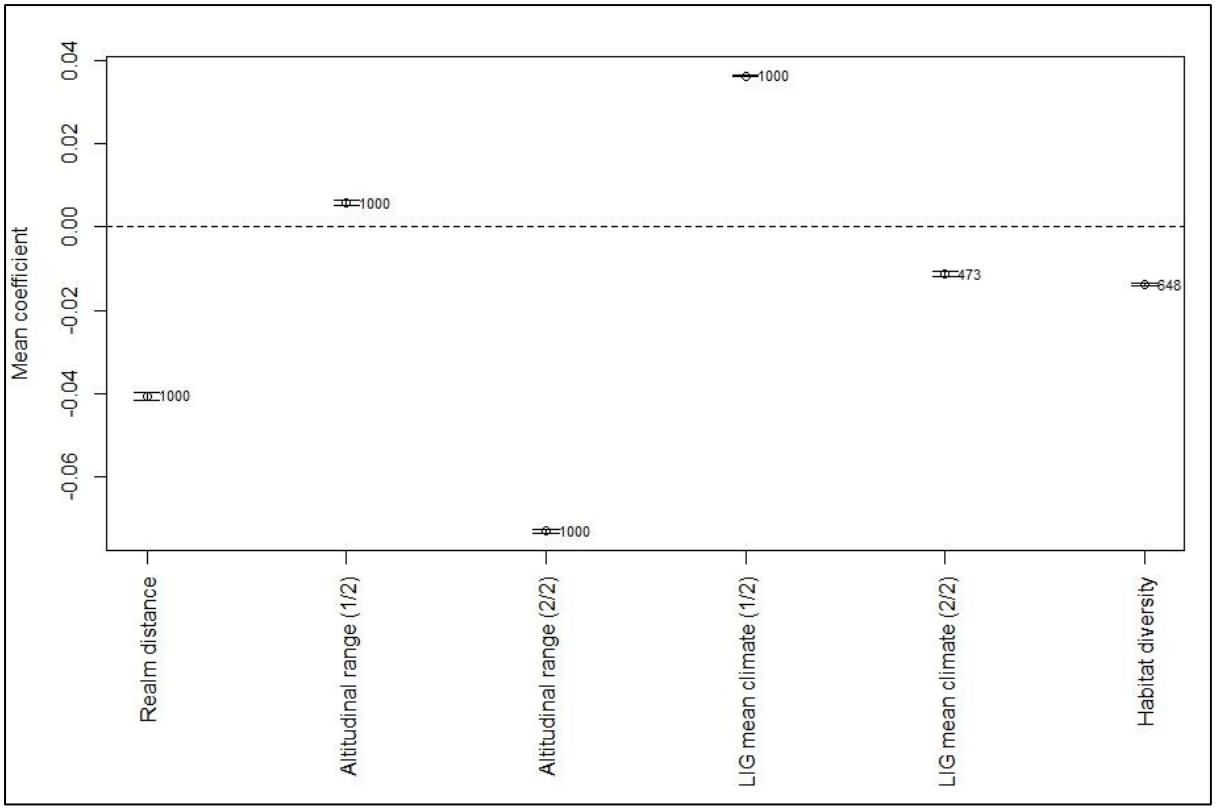

Figure S6.5: The mean coefficients (+/- 95% confidence intervals) of the full global model including: habitat diversity, neighbouring realm distance, altitudinal range, and mean climate stability (over 125 ka). Numbers alongside points indicate how often each variable was in the best model across 1000 randomly selected subsets of data. SR has been excluded from the graph to show the coefficients of the other variables more distinct.

Figure S6.6: The coefficient of variation for the mean PD derived from the 200 trees within each grid cell. Dark blue indicating cells with a low coefficient of variation, light blue areas indicating a higher coefficient of variation. Only 5% of the grid cells have a coefficient of variance of 0.06 or higher, these are mainly located in areas with very low species richness.